

Hunting, spacing and antipredatory behaviour in nymphs of *Dinocras cephalotes* (Plecoptera)

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Lund 1983

Organization LUND UNIVERSITY Department of Animal Ecology Ecology Building Helgonavägen 5 S-223 62 LUND	Document name DOCTORAL DISSERTATION	
	Date of issue 6 maj 1983	
	CODEN: LUNBDS/(NBZE-1023)/1-67/(1983)	
Author(s) Per Sjöström	Sponsoring organization	
Title and subtitle Hunting, spacing and antipredatory behaviour in nymphs of <u>Dinocras cephalotes</u> (Plecoptera)		
Abstract Aspects on feeding behaviour, microhabitat selection, territoriality and antipredatory behaviour in nymphs of <u>Dinocras cephalotes</u> were investigated both in their natural habitats and in the laboratory. Prey consumption during the year was investigated from gut content. Diet overlap was small between the largest and smallest nymphs as regards prey size. In large nymphs caseless caddis larvae was the dominating food in terms of weight, while chironomid larvae constituted the major part in small nymphs. The nymphs selected sizes of prey in the proportions they occurred in the environment in spite of larger prey items were shown to reduce the duration of the last instar. Microdistribution of three lotic insect predators was studied by means of multivariate statistical analysis. High abundances of caseless caddis larvae, large size of potential prey items and moss cover were variables significantly correlated with the occurrence of the predators. A searching strategy was adopted when the nymphs were hunting during darkness, while at twilight they rather were ambushers. The eyes were primarily used for the detection of predators. The nymphs showed a pronounced territorial behaviour. When resident in a retreat or in the hunting area, the nymph successfully defended these resources against intruders of equal size. When attacked by fish the nymphs were frequently ejected alive and the nymphs swam to the bottom and feigned dead. The presence of cerci did increase the probability of the nymphs being ejected as did they increase the handling time of the predator.		
Key words Dinocras cephalotes, perlid stonefly, nymph, feeding, prey size, microdistribution, hunting strategy, vision, spacing, territoriality, antipredatory behaviour.		
Classification system and/or index terms (if any)		
Supplementary bibliographical information		Language English
ISSN and key title		ISBN
Recipient's notes	Number of pages 67	Price
	Security classification	

Distribution by (name and address)

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HUNTING, SPACING AND ANTIPREDATORY BEHAVIOUR IN NYMPHS

OF DINOCRAS CEPHALOTES (PLECOPTERA)

PER SJÖSTRÖM

FK, Ld

Akademisk avhandling, som för avläggande av filosofie
doktorsexamen vid matematisk-naturvetenskapliga fakul-
teten vid Lunds universitet kommer att offentligen
försvaras å Ekologihusets föreläsningssal, Helgonavä-
gen 5, Lund, onsdagen den 1 juni 1981, kl 1300.

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DISSERTATION

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ABSTRACT

Aspects on feeding behaviour, microhabitat selection, territoriality and anti-predatory behaviour in nymphs of Dinocras cephalotes were investigated both in their natural habitats and in the laboratory.

Prey consumption during the year was investigated from gut content. Diet overlap was small between the largest and smallest nymphs as regards prey size. In large nymphs caseless caddis larvae was the dominating food in terms of weight, while chironomid larvae constituted the major part in small nymphs.

The nymphs selected sizes of prey in the proportions they occurred in the environment in spite of larger prey items were shown to reduce the duration of the last instar.

Microdistribution of three lotic insect predators was studied by means of multivariate statistical analysis. High abundances of caseless caddis larvae, large size of potential prey items and moss cover were variables significantly correlated with the occurrence of the predators.

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TACK

En mängd personer har på olika sätt bidragit till färdigställandet av denna avhandling. Staffan Ulfstrand var min handledare under de första åren och det var han som fick mig intresserad av bäcksländor och då särskilt Dinocras. Per Brinck, min nuvarande handledare, har kritiskt granskat mina manuskript men även genom sin uppmuntran och med sin omfattande kännedom om bäcksländor, bidragit till att öka min förståelse för dessa djurs ekologi. Mina vänner i rheoekologiska gruppen har bidragit till en vänlig och stimulerande arbetsmiljö samt har alltid varit beredda att diskutera problem och att kritiskt läsa manuskript. Dan Nilsson hjälpte mig med de optiska mätningarna. Oumbärliga för det slutliga färdigställandet av avhandlingen har varit Steffi Douwes, Ylva Zachrison och Gunilla Lindquist. Astrid Ulfstrand ritade den Dinocras nymph som pryder omslaget. Till alla dessa och en mängd inte nämnda riktar jag ett varm tack. Ett särskilt tack vill jag dock rikta till min hustru och mina barn utan vilkas tålamod denna avhandling ej varit möjlig.

LIST OF PAPERS

The thesis is based on the following papers:

- I Sjöström, P. Prey consumption by nymphs of Dinocras cephalotes (Plecoptera). - Manuscript.
- II Malmqvist, B. and Sjöström, P. 1980. Prey size and feeding patterns in Dinocras cephalotes (Plecoptera). - Oikos 35: 311-316.
- III Malmqvist, B. and Sjöström, P. Does prey size influence the microdistribution of lotic insect predators? - Manuscript submitted to Freshwater Biology.
- IV Sjöström, P. Hunting behaviour in nymphs of Dinocras cephalotes (Plecoptera). - Manuscript.
- V Sjöström, P. Territoriality in nymphs of Dinocras cephalotes (Plecoptera). - Manuscript.
- VI Otto, C. and Sjöström, P. 1983. Cerci as antipredatory attributes in stonefly nymphs. - Oikos (in press).

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BACKGROUND AND SUMMARY OF RESULTS

In this thesis I try to elucidate some aspects on the ecology of nymphs of Dinocras cephalotes. The first papers are primarily dealing with the feeding ecology and microdistribution of the nymphs, while the later papers are more focused on behavioural aspects. D.cephalotes is the only member of the family Perlidae occurring in Sweden. It is our largest stonefly and an effective predator on invertebrate prey. The distribution is rather patchy but nymphs occur in streams from the far north to the southern parts of the country.

The nymphs inhabit small to medium sized streams with a stony substrate, the stones being rather loosely attached to the bottom, thereby creating suitable crevices in which the nymphs can hide during the light hours.

All nymphs, either they were studied in situ or used for experiments in the laboratory, were collected in The Klöva stream situated in the province Scania in southernmost Sweden.

RESULTS

The feeding of the nymphs was studied during one year by means of gut analyses (Paper I). Small nymphs fed mainly on chironomid larvae, while medium sized nymphs included more stonefly and mayfly nymphs in their diet. In the largest nymphs caseless caddis larvae constituted, in terms of weight, a major part of the diet. There was a positive correlation between the size of the predator and the size of the consumed prey. The large nymphs did not include small specimens of stoneflies, mayflies and caddis larvae in their diet. Thus, as regards prey size, the diet overlap between small and large nymphs was low. This lack of size overlap could indicate either an active prey size selection by larger nymphs or segregation of microhabitats by the different sized nymphs.

The propensity to select between different prey sizes was investigated in Paper II. When the nymphs were supplied with large prey specimens they emerged earlier compared to nymphs supplied with only small prey. The nymphs, however, did not select these large sized prey items, but rather consumed the different sizes of prey in proportion to their occurrence in the environment.

The microdistribution of the nymphs was assessed using a multivariate statistical analysis (Paper III). Factors pertaining to the prey community showed to be the most important variables correla-

ted to the occurrence of the nymphs. For large nymphs, the densities of caseless caddis larvae and large sized stonefly prey were the most important factors, while the variables most strongly correlated to the distribution of small nymphs were the density of Hydropsyche siltalai and the percentage moss cover on the stones. In Paper IV the hunting behaviour during darkness and twilight was studied. Attacks were released when the nymphs encountered the prey with the antennae or the hair fringes on the tibiae in darkness as well as in twilight. At twilight, the nymphs showed a higher propensity to pursue the prey after a missed attack. The nymphs changed strategy from being searchers at darkness to ambushers at twilight. The optical design of the eye revealed that those parts of the eye that were optimized to the light regimes at which the nymphs were preferably active were directed upwards and backwards, thus implying their main function to be the detection of predators.

Nymphs of equal size showed pronounced territorial behaviour (Paper V). The nymphs defended resources, i.e. retreats and hunting area against intruding nymphs. The one first in possession of the resources won most of the contests with intruders. The intruding nymph, however, successfully contested ownership of suboptimal retreat against both the dominating nymph and subsequent intruders.

When attacked by a fish predator many nymphs were not devoured but ejected alive (Paper VI). As soon as they were ejected the nymphs showed a propensity to swim downwards and when in contact with the bottom they became motionless. This behaviour was most successful in preventing the predator to perform a new attack as fish predators seldom distinguish a motionless prey. The cerci acted as obstacles when the fish attacked from behind and both handling time and the proportion of nymphs ejected increased when the attacks were performed from this direction.

PREY CONSUMPTION BY NYMPHS OF DINOCRAS CEPHALOTES (PLECOPTERA)

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ABSTRACT

The contents of the proventrikel was analyzed and the size of the ingested prey calculated for nymphs of the perlid stonefly Dinocras cephalotes, collected once a month during one year.

Chironomid larvae constituted the major part of the food of the small nymphs, while mainly mayfly nymphs and stonefly nymphs were consumed by the middle sized Dinocras nymphs, and caseless caddis larvae predominated in the guts of the largest nymphs.

The size of the ingested prey increased as the predator grew larger. Diet overlap values indicated that the largest Dinocras nymphs excluded the smallest prey items from their diet in all prey categories except the chironomid larvae where the predator rather expanded the size range of ingested prey as it grew larger.

INTRODUCTION

Perlid stonefly nymphs are in general viewed upon as being unselective in their choice of prey. Consequently, the abundance and diversity of the benthic fauna are reflected in their diet (Hynes 1941, Siegfried and Knight 1976a, Allan 1982). Mackereth (1957) and Minshall and Minshall (1966) suggested, however, that some species of carnivorous stoneflies select their prey rather than accept any available abundant prey.

Several investigators have found a positive correlation between predator size and size of prey ingested by perlid stonefly nymphs (e.g. Sheldon 1969, Winterbourn 1974, Mouthon and Verneaux 1979) i.e. a selection for prey size rather than prey species. Allan (1982) suggests that such correlations might be artifacts caused by juxtaposition of the life cycles of the predators and their prey i.e. larger size classes of the predators tend to cooccur with larger size classes of the prey. In a laboratory study, nymphs of the perlid stonefly Dinocras cephalotes (Curtis) were provided different sizes of the mayfly Baetis rhodani (Pict.), but no size selective predation was found (Malmqvist and Sjöström 1980).

Size variation within or size differences between lotic predatory species has been suggested to reduce intra- and inter-specific competition and maximize resource utilisation (Macan 1958, Hynes 1961). This could be obtained in three ways: either by size or species dependent prey selection or by habitat segregation of the different sizes or species of the predators (Sheldon 1969).

The present study is focused on whether D. cephalotes nymphs, in the field, show size dependent patterns in their prey consumption in terms of prey species or prey size. If there exists a

positive correlation between predator and prey size, is it then merely because of an expansion of the size range of prey consumed?

MATERIAL AND METHODS

The life cycle of D. cephalotes usually lasts for three years (Hynes 1941, Brinck 1949). The nymphs inhabit small to medium sized streams with swift flowing water.

The study was carried out in the Klöva stream in the western part of the province Scania in southernmost Sweden. The stream runs through a ravine surrounded by deciduous forest consisting mostly of beech (Fagus silvatica L.) and alder (Alnus glutinosa L.).

Nymphs of D. cephalotes were collected in a riffle with swift flowing water and a substratum of boulders and stones, rather loosely attached to the bottom. Sampling was performed at about monthly intervals from September 1976 through August 1977.

The nymphs were immediately preserved in 70 % ethanol. Length and interocular distance were measured under a dissecting microscope and the nymphs were sexed. The foregut content was examined and the prey items, whenever possible, identified to species level or to lowest possible taxon. The head width of the ingested prey specimens was measured when possible.

To facilitate a comparison of the diet in differently sized Dinocras nymphs they were grouped in four size categories with the following ranges in interocular distances: I < 1.9 mm, II 2.0 - 2.9 mm, III 3.0 - 3.9 mm and IV > 4.0 mm. The first three size categories correspond roughly to the first, second and third year old nymphs, respectively, while size category IV comprises full grown female nymphs.

In order to quantify overlaps in diet between the different size groups of Dinocras both in terms of prey species and prey size Schoener's (1968) index was used:

$$D = 1 - \frac{1}{2} |p_{ix} - p_{iy}|$$

where p_{ix} and p_{iy} are the intensities of utilisation of the i th resource (prey size or prey species) by the size categories compared, x and y , of Dinocras nymphs.

Correlations between head width and weight (60° C dry weight) were made for each of the four major groups of prey, viz. Ephemeroptera, Plecoptera, Trichoptera and Diptera, commonly found in

the guts of Dinocras nymphs. The prey specimens used for this correlation were sampled at one single occasion in May.

RESULTS

The size frequency distribution of the Dinocras nymphs during the year, examined for each sex, showed no clear size cohorts referring to a life cycle of three years (Fig. 1). Small nymphs were present during most of the year.

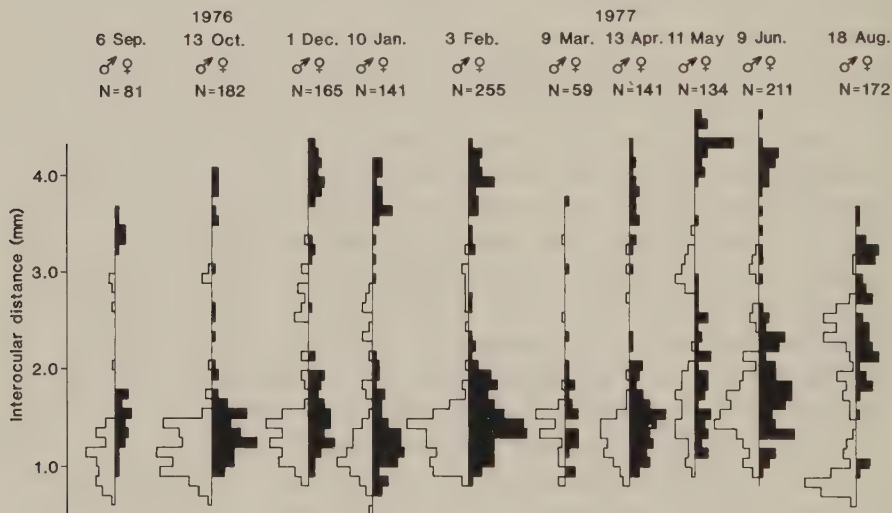


Fig. 1. Size frequency distribution of female nymphs (black) and male nymphs of Dinocras cephalotes from September 1976 through August 1977.

Dinocras nymphs ingested a wide range of prey species (Tab. 1). In terms of number, chironomid larvae were the dominating food item. Mayflies mainly Baetis rhodani, showed no seasonal occurrence in the diet except for a slight decrease in winter. Blackflies were found in the diet mainly during summer and early autumn, while stoneflies and caddis larvae (mainly species belonging to the families Hydropsychidae and Polycentropodidae) were consumed at a minimum during summer. Ingestion of the amphipod Gammarus pulex (L.) was generally low, and since this prey occurred in the guts as fragments only, it was impossible to obtain any size measurements. Remains of D. cephalotes nymphs were observed a few times, but cannibalism does not seem to be of great importance in the

TABLE 1

Seasonal variation in gut content of Dinocras cephalotes, given as percentages of the total number of food items in the guts.

Food items	Sep	Oct	Dec	Jan	Feb	Mar	Apr	May	Jun	Aug
<i>Amphipoda</i>										
<i>Gammarus pulex</i>	5	14	5		8		12	6	0.5	
<i>Ephemeroptera</i>										
<i>Baetis rhodani</i>	21	19	3	12	9	40	17		21	39
<i>Heptagenia sulphurea</i>	2		0.5	3	1	2				1
Unidentified						3			2	4
<i>Plecoptera</i>										
<i>Brachyptera risi</i>				3	2	5	12	3		
<i>Amphinemura sulciatilis</i>				3	1			10		
<i>Nemoura flexuosa</i>					1			11		
<i>Leuctra</i> spp.	2			3			4			2
<i>Capnia bifrons</i>				4	2					
<i>Dinocras cephalotes</i>			0.5					3		
Unidentified		16	3	4	1	4	4	9	0.5	1
Trichoptera	5	35	8	15	17	4	17	14	7	5
Simuliidae		3	0.5	1	5	2	4	11	6	23
Chironomidae	64	5	79	51	52	40	17	13	56	23
Unidentified material	2	8	1	1	1		12	19	7	2

Empty guts (%)	38	41	2	28	13	21	58	38	46	20
Dinocras analysed (N)	29	49	59	54	56	34	37	65	91	36

feeding of Dinocras nymphs. Fragments of plants, detritus and algae were found, but in no case did this fraction dominate the gut content. The vegetable matter made up such an insignificant proportion of the total matter ingested that it could well be assigned to the gut contents of the prey.

The proportion of empty guts varied between 2 and 58 per cent (Tab. 1) with a minimum in winter.

The proportion of the four major groups of prey in the guts changed with the size of the Dinocras nymphs (Fig. 2). Chironomid larvae were the numerically dominating food item in all the four size groups of the predator, though in diminishing proportion in the larger nymphs. Caddis larvae and stonefly nymphs increased correspondingly as the predator grew larger, while most mayfly nymphs were consumed by the middle sized Dinocras nymphs.

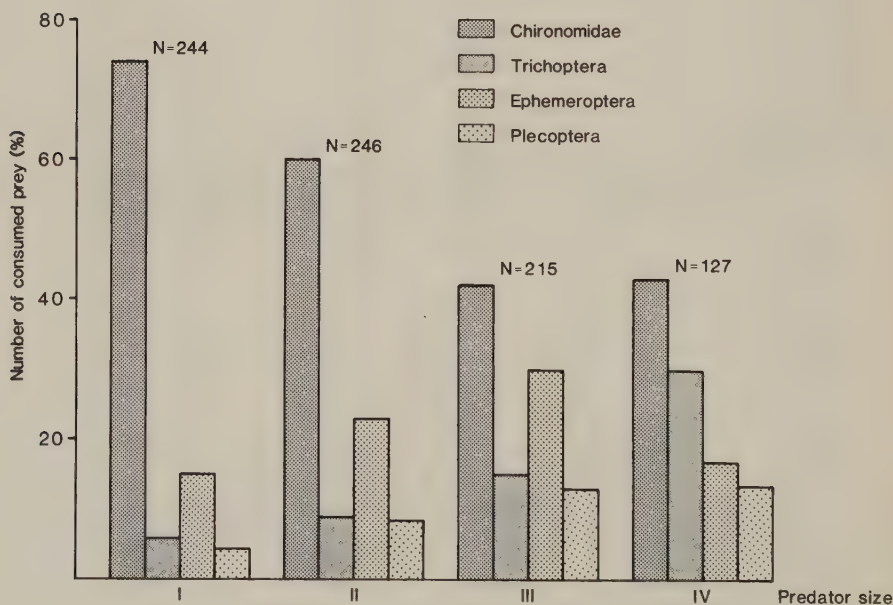


Fig. 2. Distribution of prey items in numbers in the guts of four size categories of Dinocras cephalotes nymphs.

The dry weight of the consumed prey is, however, a more realistic way to show the relative importance of different prey as food than to record numbers. When head widths of ingested prey items were recalculated as dry weights, based on the mean weight of complete animals, the importance of the caddis larvae as food was strengthened (Fig. 3). Chironomid larvae constituted a minor proportion except in the smallest size group of the predator, while nymphs of stoneflies and mayflies remained the most important prey for the middle sized predators (Fig. 3).

Mean gut content, in terms of dry weight, increased with a factor of about 20 from the smallest to the largest size group of the predator (Tab. 2), the individuals with empty stomachs excluded.

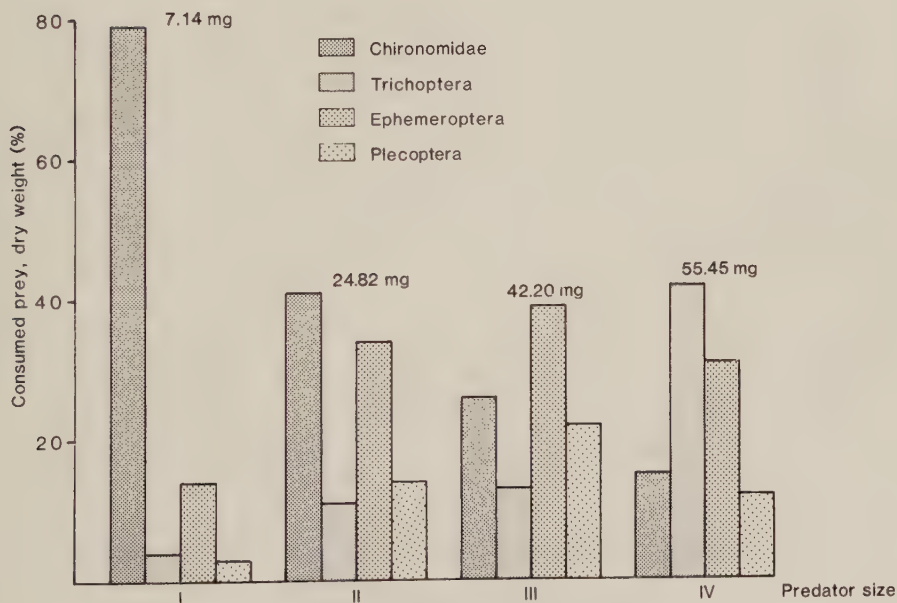


Fig. 3. Distribution of prey items, calculated as dry weight of total gut content in four size categories of Dinocras cephalotes nymphs.

TABLE 2

Variation in gut content, expressed as mg dry weight, in different size groups of Dinocras cephalotes. The dry weights were calculated from correlations of head width and dry weight of complete specimens of the taxa.

Size group of predator	Number of predators (N)	Mean dry weight gut ⁻¹ (mg)	S.D.
I	205	0.071	± 0.074
II	122	0.348	± 0.306
III	120	0.597	± 0.599
IV	63	1.136	± 1.213

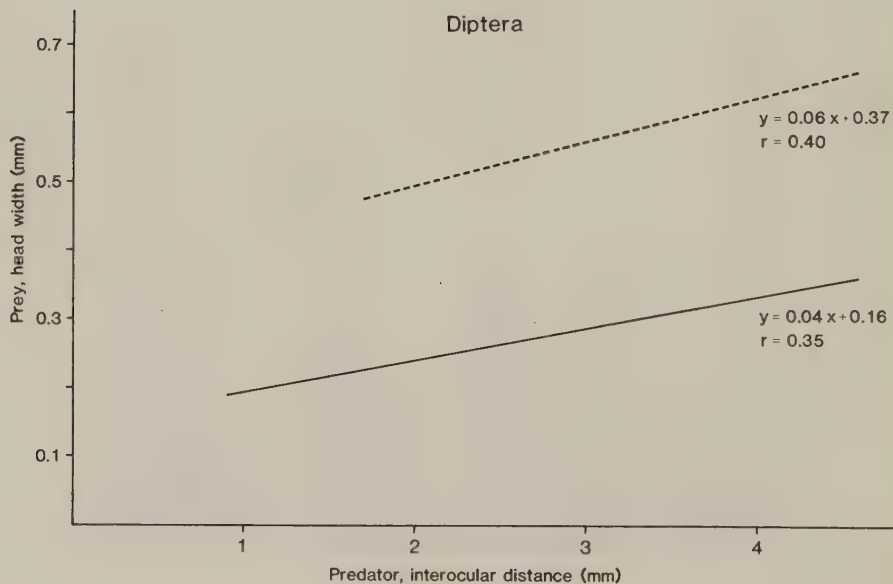


Fig. 4. The size of Dinocras cephalotes nymphs in relation to the size of ingested Diptera larvae. Chironomid larvae solid line (N = 470) and simuliid larvae broken line (N = 52).

Predator size and size of prey were positively correlated in the four groups of prey (Figs 4-7), though for the chironomid larvae the correlation was weak ($r = 0.35$).

The analysis of diet overlap (Tab. 3) indicated that prey was not selected on taxonomic units but rather with regard to the size of the prey. The overlap decreased when the size differences of the predator increased and became small or nonexistent when the smallest and largest size categories of the predator were compared. Least overlap in size of consumed prey was found within Trichoptera and Plecoptera, while for chironomid larvae there was a pronounced overlap between all the sizes of Dinocras nymphs (Tab. 3).

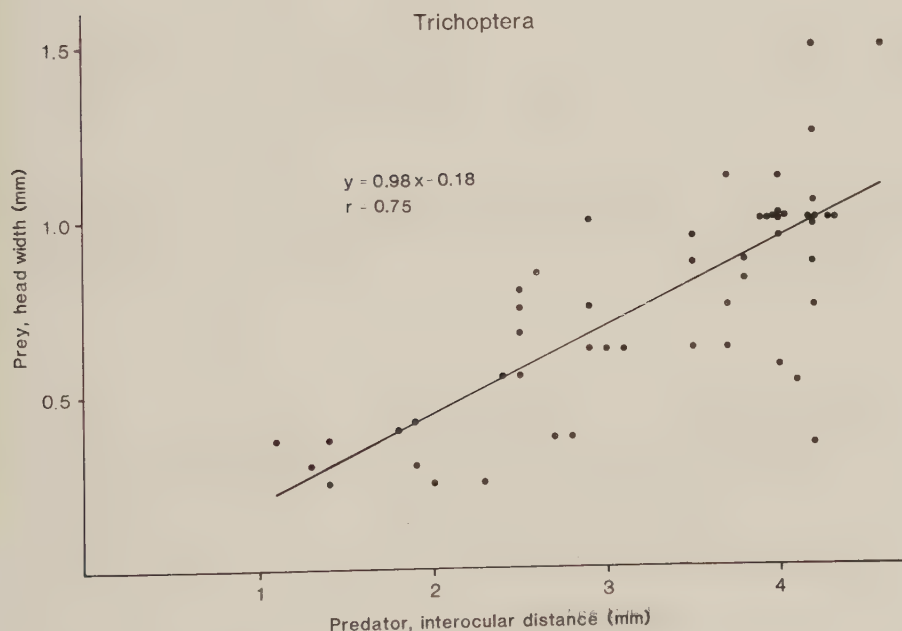


Fig. 5. The size of Dinocras cephalotes nymphs in relation to the size of ingested Trichoptera larvae.

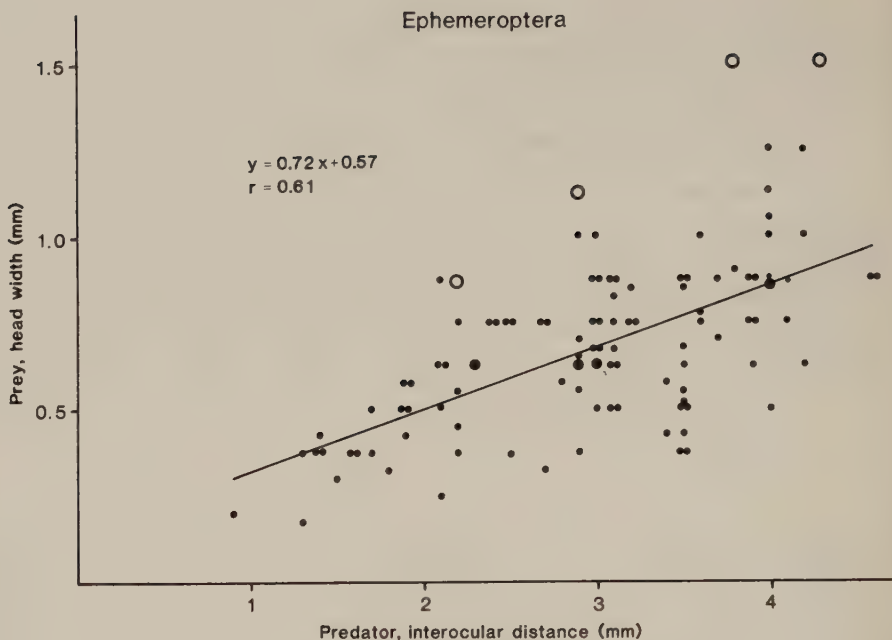


Fig. 6. The size of *Dinocras cephalotes* nymphs in relation to the size of ingested Ephemeroptera nymphs. Open circles denote *Heptagenia sulphurea*. Large filled circles denote 5 individuals.

DISCUSSION

The seasonal variation in feeding habits of *D. cephalotes* nymphs is in accordance with that found in other perlid stonefly nymphs (e.g. Sheldon 1969, Siegfried and Knight 1976). This probably reflects the availability of prey species rather than selection for certain species of prey (Siegfried and Knight 1976a, Allan 1982).

Ingestion of various amounts of detritus and pland material seems almost universal among lotic predatory insects. This trend towards omnivory might be related to fluctuating food resources (Coffman et al. 1971, Siegfried and Knight 1976b). *D. cephalotes* nymphs, however, seem to be strictly carnivorous in all sizes. This is in accordance with the results of Berthelemy and Lahoud (1981).

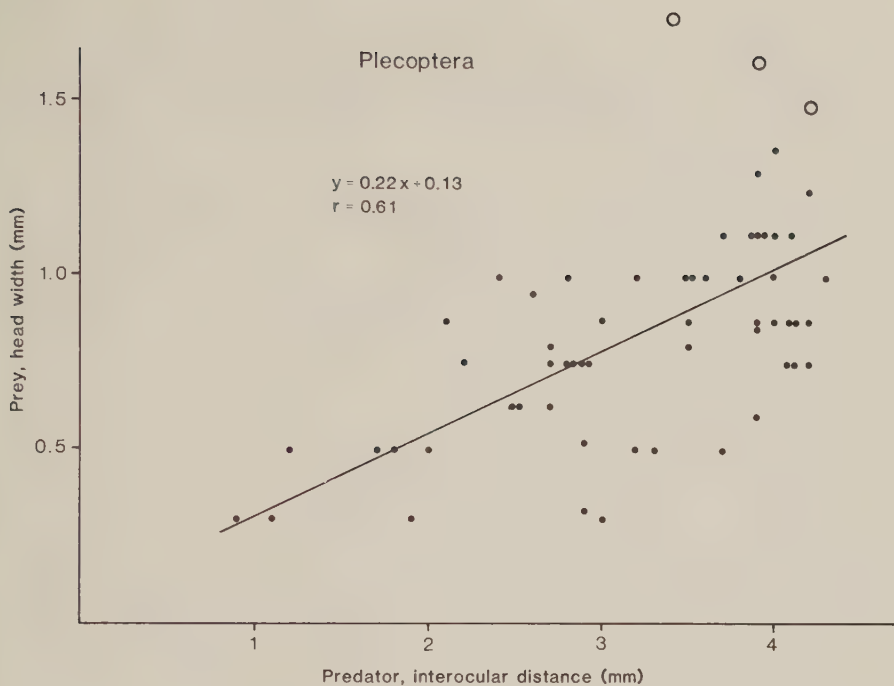


Fig. 7. The size of Dinocras cephalotes nymphs in relation to the size of ingested Plecoptera nymphs. Open circles denote ingested Dinocras nymphs.

TABLE 3

Diet overlap values comparing different size groups of Dinocras cephalotes nymphs with taxonomic grouping and size of prey items. The number of categories used in the taxonomic analysis is 15.

Diet overlap	Size groups of predator					
	I-II	I-III	I-IV	II-III	II-IV	III-IV
Taxonomic	0.78	0.65	0.55	0.80	0.71	0.85
Chironomidae	0.80	0.62	0.58	0.78	0.73	0.91
Trichoptera	0.35	0	0.05	0.65	0.47	0.55
Ephemeroptera	0.29	0.14	0.16	0.81	0.44	0.58
Plecoptera	0.19	0.25	0	0.53	0.48	0.75

The proportion of empty guts was at a minimum during winter. This might be due to the lower temperature and consequently longer retention time of ingested prey. An additional explanation could be the extensive consumption of chironomid larvae during this time of the year.

Sheldon (1969) showed that in Arcynopteryx californica (Banks), the large nymphs fed mainly on caddis larvae, the middle sized nymphs on stonefly and mayfly nymphs, while the smallest nymphs to a large extent consumed chironomid larvae. A similar feeding pattern was found for D. cephalotes nymphs in the Klöva stream.

The large spectrum of prey species found in the guts is in accordance with the observations made by Hynes (1941) and Brinck (1949), though the above mentioned four groups of prey dominated the diet.

From an energetic point of view, it should be advantageous for the nymphs to consume as large prey as possible. Malmqvist and Sjöström (1980) found that a high proportion of large prey items included in the diet of large D. cephalotes nymphs shortened the duration of the last nymphal instar. It is true that chironomid larvae, in terms of number constituted a considerable part of the diet in all size classes of Dinocras nymphs, but in terms of dry weight, caddis larvae constituted a major part of the diet in large nymphs. The mean dry weight of the chironomid larvae consumed by the largest nymphs was 0.06 mg, but for caddis larvae 1.06 mg. Thus, from an energetic point of view, it requires some 20 chironomid larvae to match one caddis larva, the costs of searching and handling the prey excluded.

There is some controversy on whether carnivorous stonefly nymphs expand the size range of captured prey as they grow larger or if they rather select larger prey (Sheldon 1969, 1980, Allan 1982, Peckarsky 1982). In Dinocras the diet overlap between small and large nymphs was considerable with respect to species of prey. Similarly, there was great overlap as regards prey size in the group Chironomidae. The lack of size overlap, when comparing small and large nymphs, within the other prey groups, might indicate a selection for larger prey. However, Dinocras nymphs did not select larger prey sizes in a laboratory study (Malmqvist and Sjöström 1980), which might indicate rather a microhabitat segregation by different sized Dinocras nymphs.

ACKNOWLEDGEMENTS

I thank Prof. P. Brinck, Drs. B. Malmqvist, L.M. Nilsson and C. Otto for helpful comments on the manuscript. I am also grateful to Mrs. S. Douwes who drew the figures and to Mrs. Y. Zachrisson who typed the manuscript.

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Prey size and feeding patterns in *Dinocras cephalotes* (Plecoptera)

Björn Malmqvist and Per Sjöström

Malmqvist, B. and Sjöström, P. 1980. Prey size and feeding patterns in *Dinocras cephalotes* (Plecoptera). – Oikos 35: 311–316.

In laboratory experiments nymphs of the predatory stonefly *Dinocras cephalotes* (Curtis), supplied with large individuals of the prey *Baëtis rhodani* (Pict.), emerged earlier than nymphs fed with small individuals of the mayfly. Early emergence, within certain limits, may be advantageous to the stonefly. The stonefly nymphs did not select prey of the most favourable size, probably because of their hunting technique. Small predators were able to kill large prey, but frequently left heavily sclerotized parts of large mayfly nymphs. During the last instar feeding was initially low, but increased to a maximum after a few days. Feeding thereafter decreased slowly and almost ceased several days before emergence. A similar pattern, although not so expressed was noted in earlier instars. Generally, food intake was pulsed with maxima every 2.5–4 d.

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В лабораторных опытах нимфы хищных веснянок *Dinocras cephalotes* (Curtis), выращенные крупными особями *Baëtis rhodani* (Pict.), заканчивали развитие раньше, чем нимфы, питавшиеся мелкими поденками. Ранний вылет в определенных пределах может быть выгоден для веснянок. Нимфы веснянок не избирательны к жертвам любого доступного размера вероятно по причине способа своей охоты. Маленькие хищники могут убить крупную жертву, но часто оставляют сильно склеротизованные части крупных нимф поденок. В последнем возрасте активность питания сначала низка, а затем повышается до максимума в течение нескольких суток. Затем она медленно снижается и почти прекращается за несколько дней до имагинальной линьки. Подобная динамика, но менее выраженная, отмечена и у младших возрастов. В целом скорость потребления пищи колеблется, с максимумами через каждые 2,5 – 4 дня.

Accepted 11 February 1980

© OIKOS 0030-1299/80/060311-06 \$02.50/0

Introduction

Several studies have concerned prey selection and feeding strategies of carnivorous stonefly nymphs. Some authors have described them as unselective generalists in terms of size (Siegfried and Knight 1976a, Devonport and Winterbourn 1976) and species (Hynes 1941, Siegfried and Knight 1976b) of the prey. Others, however, found indications of selectivity (Mackereth 1957, Minshall and Minshall 1966, Sheldon 1969, Moulton and Verneaux 1979).

If selectivity of the predator with respect to prey size exists, the question could be raised whether the predator has the ability to "switch", that is, to consume the most abundant prey species or prey size present in a proportion higher than actually occurs in the environment (Murdoch 1969). Such switching behaviour may act as a community stabilizing mechanism as prey categories will be preyed upon only when numerous in relation to others. There have been few studies concerning switching in insect predators. Lawton et al. (1974) found a clear tendency for switching behaviour in the water bug *Notonecta* when offered two prey species in different proportions. In starved damselfly naiads, *Anomalagrion hastatum*, switching was observed when offered two cladoceran prey species (Akre and Johnson 1979).

The questions focussed upon in this study include: How does prey size influence prey selection in differently sized *Dinocras*? Does switching occur? What is the relationship between numbers and size of prey and energy gain? Does the predator feed continuously when prey is very abundant?

We used nymphs of the large perlid stonefly *Dinocras cephalotes* (Curtis) for our experiments. The species is widespread in streams with swift current and stony substratum, is strictly carnivorous, and investigated populations have a life cycle lasting for three years. Its hunting is restricted to the dark period.

Nymphs of *Baëtis rhodani* (Pict.) (Ephemeroptera) were chosen for prey, partly because this species is commonly found in *Dinocras* guts (Sjöström unpubl.), and partly because it is easy to collect in large numbers.

Material and methods

Two experiments were conducted, the first of which was started on 11 April 1978, using three year old *Dinocras* nymphs, collected from a small stream in southernmost Sweden. The emergence of this species normally occurs in June, and the nymphs collected were expected to moult into the last instar during the course of the experiment. The nymphs were placed, singly, in 35 plastic aquaria measuring 120 × 120 × 120 mm. On the bottom a ceramic plate (100 × 100 mm) was put on top of 4 small stones (approx. diam. 10 mm) to provide a suitable and reproducible environment for the insects.

To create a current and avoid oxygen deficiency, air was pumped at a relatively high pressure through an airstone in each aquarium. Natural light conditions were simulated. A pilot study showed 20 individuals of *Baëtis rhodani* to be sufficient in order to avoid food shortage. The prey organisms were sorted by eye into "large" and "small" individuals, medium sized ones being discarded. The prey organisms were introduced in 5 replicates of 7 different combinations of small/large *Baëtis* nymphs: 0/20, 4/16, 8/12, 10/10, 12/8, 16/4, and 20/0. Since the size division was subjective, there were minor differences in size within the two size groups. In a calorimetric analysis (wet oxidation, Maciolek 1962) the average energy content of a large individual (23.9 J) was found to be about 5 times that of a small one (4.9 J). The number of surviving nymphs and carcasses was counted every morning for 70 consecutive days. New mayfly nymphs were added as required to keep the number constant and those showing signs of imminent emergence (dark wing-pads) were also replaced. Moulting and emergence was also registered. The temperature (Fig. 1) was controlled by means of tap water cooling around the aquaria. Tap water temperature corresponded well with field conditions, except for the first two weeks, when it was slightly higher in the laboratory.

The second experiment was performed in 1979 using the same experimental set-up. This time both two and three year old *Dinocras* nymphs were used, and the temperature was kept constant at 10°C. In this experiment no mixtures of prey sizes were used, either large or small prey being offered to the stonefly nymphs.

Results

The time distribution of last moulting and emergence in the *Dinocras* nymphs is shown in Fig. 1.

Stonefly nymphs often only partly devoured their prey. In particular small *Dinocras* offered large mayflies often refused to eat the thorax region and the head of the prey.

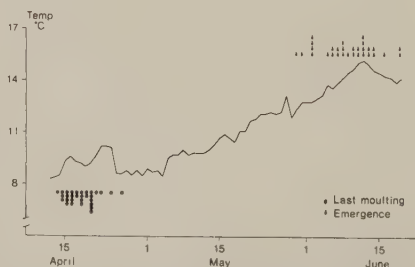


Fig. 1. Moulting and emergence in last instar *Dinocras cephalotes* in relation to temperature in the 1978 experiment.

To test if *Dinocras* showed any switching behaviour when offered large and small prey animals in different proportions, the following formula given by Murdoch (1969) was applied:

$$Y = \frac{100cX}{100 - X + cX}$$

where X is the number of prey in the environment and Y the number eaten. c is a proportionality constant indicating the preference for one of the prey categories determined from the observations in those aquaria containing 50% of each prey size. c was found to be 1.17 in this experiment. The result is graphically presented in Fig. 2. No significant deviation from the non-switching model can be detected.

A significant correlation was established between the duration of the last larval instar and the amount of consumed prey in terms of energy (Fig. 3).

When the proportion of large prey to small prey in the diet exceeded 1:1 there was a marked decrease in the number of days needed for emergence (Fig. 4). In younger nymphs, however, instar duration was not changed by different diets.

The actual intake of energy per day per individual predator decreased linearly with increasing proportion of small prey in the environment (Fig. 5); the intake was lower in male than in female stoneflies.

Further, a positive relationship was established between the predator's size and the number of prey eaten (Fig. 6). Large predators consumed small prey animals in numbers about 70% higher than large prey items,

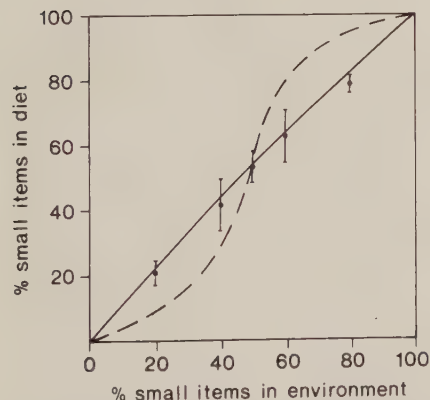


Fig. 2. A switching experiment. The solid line indicates the response expected if switching does not occur and the broken line if it occurs. The points denote the mean values of the observed results and the vertical bars the standard deviations.

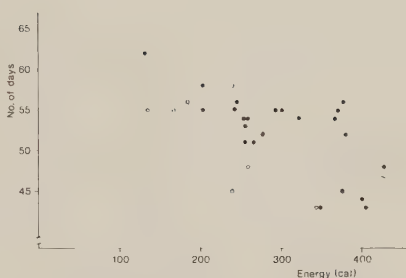


Fig. 3. The relationship between amount of energy consumed by *Dinocras cephalotes* during the period from the last moulting to emergence and duration of the last nymphal instar in males (open points) and females (solid points). The regression line has the equation $y = -0.037X + 62.59$ ($r = -0.59$).

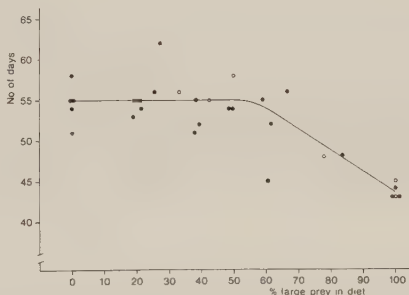


Fig. 4. The relationship between percentage distribution of size of prey items consumed and duration of the last nymphal instar in males (open points) and females (solid points).

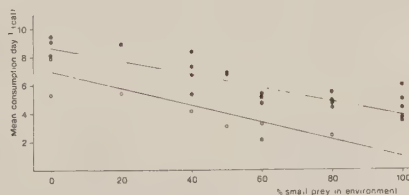


Fig. 5. Mean energy intake per day by last instar *Dinocras* nymphs when large and small prey items were offered in different proportions. The regression line for females (solid points) is $y = -0.04X + 8.64$ ($r = -0.79$) and for males (open points) $y = -0.05X + 6.49$ ($r = -0.89$).

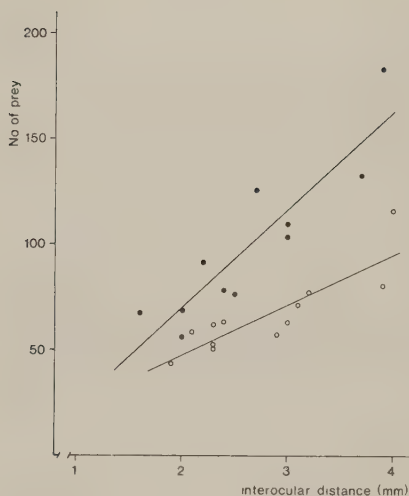


Fig. 6. Number of prey items consumed in relation to the size of *Dinocras* nymphs between two successive moultings (young nymphs) or between last moulting and emergence. The points are derived from the 1979 experiment when the nymphs were fed with either small or large prey items. The regression line for small prey (solid points): $y = 46.13x - 22.64$ ($r = 0.89$) and large prey (open points): $y = 23.70x + 0.11$ ($r = 0.86$).

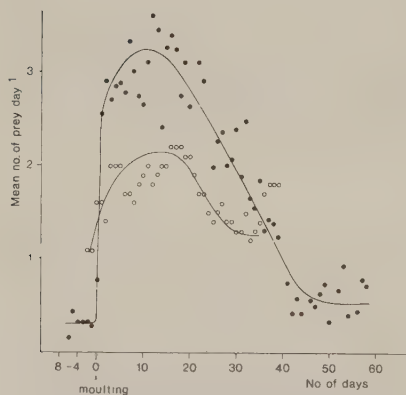


Fig. 7. Changes in consumption during last instar (solid points) and between moulting in earlier instars (open points) by *Dinocras cephalotes*.

while in small *Dinocras* consumption of small *Baëtis* in relation to large ones was only about 40% higher.

Some interesting patterns were observed in the feeding intensity between consecutive moultings of the two year old nymphs and also during the last instar in three year old nymphs. After moulting food intake was initially low, and then in a few days increased to a maximum. During the final part of the last instar the food intake, generally dropped to almost zero several days before emergence. This is shown in Fig. 7 for the 1978 experiment. The same pattern recurred in the 1979 experiment. In younger stages the initial increase and the later decrease in food intake was not that striking. Looking at each individual food intake was characterized by being pulsed with intervals between the peaks of 2.5–4 d.

Discussion

The lack of switching in *Dinocras cephalotes* could possibly be explained by its hunting method. Like other carnivorous stonefly nymphs *Dinocras* is reported to hunt mainly by means of tactile stimuli (Hynes 1941, Brinck 1949, Chisholm 1962), that is, the predator must come in direct contact with the prey animal and capture it before deciding whether it is favourable or not. If handling time is proportionally short, it would be a waste of energy to release an already captured prey and continue searching for a more rewarding one. One of the suggested factors for switching to be rewarding is that the predator's method of attack should vary between different prey objects (Murdoch 1969). This suggestion is based on the condition that learning takes place, so that it should be more efficient for the predator to use only one method rather than frequently changing between two or more.

Our results only concern different sizes of one prey species so that the possibility of switching between different prey species is not considered here. In addition, we used only single predator individuals in each aquarium. An increased predator density could possibly have affected the feeding patterns.

Our experiments did not indicate any selection for particular prey sizes in large *Dinocras* nymphs which implies that they expanded their prey size ranges rather than selected a particular size.

The experiments were not designed to explore whether the small nymphs selected any particular prey size. There did not, however, seem to be any physical restraints in capturing large *Baëtis*. Carnivorous stoneflies have been previously reported to leave large sclerotized parts uneaten (Minshall and Minshall 1966, Winterbourn 1974), which illustrates the danger of relying solely on gut analyses for the determination of prey selection.

The relationship between predator size and the number of *Baëtis* consumed (Fig. 6) does not simply

reflect the five times higher energy content of large *Baëtis* compared to small ones, but also includes different time and energy costs in coping with the differently sized prey items. Only a slightly higher number of small prey compared to large ones were consumed by both small and large *Dinocras*. Two explanations are possible: so much energy may be expended in finding several small prey items that full energy compensation is not gained while the large prey animals may be energetically relatively more costly to cope with, indicating that a large *Baëtis* may well be equivalent to about one and a half small ones.

The reduced duration of the last instar in nymphs of *Dinocras* that consumed only or to a high proportion large *Baëtis* (Fig. 4), implies that large prey items were more favourable than small ones. This means that the first alternative above is the most likely for last instar *Dinocras*. In younger instars, however, no difference in growth rate, as reflected by moulting intensity, was observed.

Early emergence in *Dinocras* is considered advantageous for mating. As soon as the environmental prerequisites for emergence are set, i.e. temperature and light, it is better to be early than late in a favourable environment. The adult stonefly which emerges early can wait for a partner to emerge and be ready to mate. On the other hand, late emergence, can reduce the chance of finding an unmated stonefly of the opposite sex.

It is well established that continuously feeding arthropods cease to feed during ecdysis (Passano 1960, Duncan and Klekowski 1975, Strong and Daborn 1980). In predatory arthropods, however, information about variations in ingestion rate in relation to the moulting cycle is less comprehensive. Haynes and Sisójevic (1966) found that female spiders fed most intensely just after ecdysis, after a few days declining to a much lower level. This is in accordance with our observation (Fig. 7). The large number of empty guts found in predatory stoneflies could partly result from this phenomenon.

The differences in the feeding pattern between last instar nymphs and earlier ones may be a result of the approaching emergence. Adult *Dinocras* do not feed. Their gut and salivary glands are atrophying and the energy gained from this process is presumably stored as fat or used in egg production (Chrisholm 1962). The decrease in consumption prior to emergence is probably due to this and other reorganization processes.

Johnson (1973) put forward the hypothesis that in a predator increased feeding rates in response to increased prey density caused individuals in different nutritional states to moult synchronously. For most of the time it would be favourable for *Dinocras* nymphs not to moult synchronously; this would reduce intraspecific competition for food. It is, however, highly beneficial to emerge synchronously. Therefore, synchronization should take place as late as possible in the

nymphal stage. It is hard to believe that the observed synchronous moulting into the last instar of *Dinocras* (Fig. 1) would be an effect of higher consumption rates considering the very low predation prior to the last moulting (Fig. 7). More probably environmental physical factors, such as temperature are involved.

In a natural situation with several prey species of different sizes *Dinocras* has the possibility of specializing. Sheldon (1969) found that the positive correlation between the size of *Acroneuria californica* (Banks) and that of its prey was explained by different choice of prey species.

Elnor and Hughes (1978) demonstrated that shore crabs, which hunt by chemical and tactile cues, chose mussels of an optimal size. When small mussels became increasingly common, however, the crabs included these small, unprofitable prey items in their diet. The authors suggested that the time to recognize and reject mussels of small size finally became so long that it no longer paid not to consume them. MacArthur and Pianka (1966) postulated that when recognition time increases more unprofitable prey items will be included in the diet. For *Dinocras* we consider that, at least in large individuals, rejecting a less profitable prey is not advantageous because the handling time probably is very short compared to recognition time. A predator hunting by sight will not only reduce recognition time but also the search time. Such a predator will therefore be more efficient and also more specialized than a predator relying mainly on non-visual stimulation. In running water many insect predators may belong to the *Dinocras*-type. Optimization of their diet is probably accomplished by selecting the microhabitat in which to hunt.

Acknowledgements – We thank Prof. S. Ulfstrand, Prof. P. Brinck and members of the Rheoecological Group in the Dept of Animal Ecology, Lund, who critically read the manuscript and suggested several improvements. Mrs. S. Douwes kindly drew the figures.

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DOES PREY SIZE INFLUENCE THE MICRODISTRIBUTION OF
LOTIC INSECT PREDATORS?

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ABSTRACT

The microdistribution of three species of insect predators in a Swedish stream was assessed using a multivariate statistical approach. Both abiotic factors and those pertaining to the prey community were included in the analysis.

The factors most strongly correlated to predator distribution were for large Dinocras cephalotes the densities of caseless caddislarvae and median weight of stonefly prey. For small D. cephalotes the density of Hydropsyche siltalai and the percentage of moss cover were most important.

Isoperla grammatica showed a significant correlation to blackfly density.

Rhyacophila nubila occurred predominantly in patches with high prey biomass and with high densities and median weight of caseless caddislarvae.

It was concluded that the quantity and quality of the prey such as size, availability, and species, might strongly influence the predators' microdistribution. The distributional pattern differs between species of predators and probably relates to different hunting strategies, i.e. degree of mobility.

INTRODUCTION

The microdistribution of benthic animals in streams has in most cases been explained by their dependence of various abiotic factors, such as current, substrate, and detritus. Recently, also biotic factors have been suggested as spatial regulators, but the combined effects of the physical and living components of the environment have rarely been accounted for (see review by Williams 1981).

In natural ecosystems the species rarely show their actual preferences for environmental parameters, but rather a pattern altered by competition and predation pressures. On the other hand, laboratory experiments never or rarely permit inclusion of the changing influence of predation and competition (cf. Sheldon & Haick 1981). In this paper, we have carried out an analysis of the realized niches of a selection of lotic invertebrate predators, aiming at an explanation of their microdistribution.

It is to be expected that the animals disperse into patches rich in their preferred food. Thus, predators should aggregate where prey is abundant or of high quality. Many other factors influence the distribution; one of the most important concerns shelter from predators. Predation is accepted as a major factor affecting the distribution and abundance of lotic animals (e.g. Reice 1981). A good way to test the truly multivariate problem of distribution within a stream section would be by using a multivariate statistical approach (Green 1974, Malmqvist 1980, Sheldon 1980, Huggins & DeBois 1981, Brönmark & Malmqvist 1982). The importance of prey quality for the predator microdistribution has, however, not been considered.

In an earlier paper (Malmqvist & Sjöström 1980) we reported that the predatory stonefly Dinocras cephalotes (Curtis) was unable to select the energetically most profitable prey in a choice between two sizes of mayfly nymphs (see also Allan 1982). It was suggested that tactile predators should hunt in a special microhabitat rather than search for a particular prey. This hypothesis implied that patches characterized by high quality prey might attract predators. Quality could be envisioned by either particularly attractive prey species, high rate of encounters, or large size of the average prey.

For analysis we selected the stoneflies Dinocras cephalotes and Isoperla grammatica (Poda), and the caseless caddisfly Rhyacophila nubila (Zett.). By multivariate discriminant analysis we sorted out the most influential factors accounting for observed distributional patterns, including qualitative characteristics such as associations to certain prey species or sizes.

MATERIAL AND METHODS

Benthic invertebrates and their substrate were sampled in a riffle section of the stream Klövabäcken in southern Sweden. In all, 47 samples were taken on 28 April, 1980. The samples were collected along eleven randomly spaced transects of a 50-metre section of the stream using a Neill sampler (area: 0.05 m^2 , mesh: 0.30 mm). Before each sample was taken, depth, current velocity (using a Kent miniflow current meter), percentage moss and filamentous algal cover were estimated. The animals were sorted under dissection microscopes at the laboratory and each animal was determined to species level, except for members of Diptera, of which only families were identified. Head width was measured for all the specimens - about 17 000 - included in the analysis. Correlations were established between head width and dry weight for each taxonomic category. The substrate was sieved and we estimated the percentages by weight of the various fractions according to the phi-scale (Cummins 1962), median particle size, and particle heterogeneity (Schwoerbel 1966). Fine and coarse particulate organic materials were arbitrarily classified into two and three categories, respectively.

For the statistical analysis the SPSS soft-ware (Nie et al. 1975) was chosen. The number of groups selected was two: presence and absence. For small Dinocras (inter-ocular distance < 1 mm) and large Dinocras (inter-ocular distance > 1 mm), however, three

groups, viz. absent, rare (1 - 2 ind.), and abundant (> 2 ind.), were found to be more adequate. The program selects the variable which causes maximum discrimination between the groups in a step-wise fashion. One limitation is that the method assumes linear variation of the variables, which often might not be the case. To account for this as far as practically possible, all variables, except for substrate variables, were logarithmically transformed ($\ln(x+1)$). Substrate characteristics are already in a logarithmic form.

The independent variables included the following environmental factors: Depth, water velocity, percentage cover of mosses and filamentous algae, and substrate characteristics, including median particle size, heterogeneity, and the percentages of different particle fractions (from < 0.25 mm diam. to > 256 mm). The biological factors included were total potential prey species densities and biomasses and the average and median biomasses per sample. In the category "potential prey species" (Tab. 1) burrowing species such as the mayfly Ephemera danica Müller, oligochaetes, and Diptera except chironomids, simuliids, and ceratopogonids, were excluded, as were well-protected species such as case-building caddisflies and the snail Ancylus fluviatilis Müller. Adult beetles were excluded since they were seldom found in the guts of the predators. Very rare species were also excluded since they were seldom found in the guts of the predators. Very rare species were also excluded since they hardly influence the distributional patterns of the predators investigated. In addition, the median size, in terms of dry weight, of the orders viz. Plecoptera (excl. Dinocras), Ephemeroptera, Trichoptera (caseless), and Diptera were included in the analyses.

RESULTS

Bivariate correlations showed that the presence of the three predator species, especially Dinocras, was positively correlated with several prey species (Tab. 1). Also with more general features of the prey category there existed significant correlations (Tab. 2). The stonefly predators showed great similarities in being correlated to prey biomass and abundances but not to the size of the prey animals. Rhyacophila nubila, in contrast, showed highly significant correlations in their distribution with such parameters as mean and median weight of potential prey animals.

This species was also positively correlated with the biomass of the prey.

Discriminant analysis has the advantage of selecting the most important variables for separating the groups which represent samples with different predator densities and at the same time the covariation between all variables is considered. For large Dinocras nymphs (inter-ocular distance > 1 mm) only biotic variables passed the significance test ($P < 0.05$) for being incorporated in the discriminant functions (Tab. 3). The first discriminant function (DF 1) was most powerful in separating microhabitats without or with low densities of Dinocras from those where it was abundant (Fig. 1A). The variables which contributed

TABLE 1

Mean densities of the most important potential prey organisms and the bivariate correlation coefficients of the relationships between their densities and those of the studied predator species. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

	MEAN DENSITY No.m ⁻²	BIVARIATE CORRELATION COEFFICIENTS			
		Dinocras		Isoperla	Rhyacophila
		large	small		
<i>Gammarus pulex</i> L.	25	-0.05	-0.16	0.06	0.09
<i>Baetis rhodani</i> (Pict.)	501	0.47**	0.56***	0.37*	0.29*
<i>Heptagenia sulphurea</i> Müll.	22	0.18	0.28	-0.09	0.35*
<i>Brachyptera risi</i> (Mort.)	10	0.52***	0.10	0.25	0.27
<i>Amphinemura borealis</i> Mort.	19	0.32*	0.41**	0.09	-0.07
<i>A. sulcicollis</i> Steph.	430	0.51***	0.53***	0.40*	0.02
<i>Leuctra fusca</i> L.	344	-0.01	0.29*	0.25	-0.15
<i>Wormaldia subnigra</i> McL.	78	0.48**	0.46**	0.20	0.24
<i>Hydropsyche siltalai</i> Döhler	95	0.54***	0.54***	0.12	0.41**
<i>Polycentropus flavomaculata</i> (Pict.)	25	0.12	-0.06	-0.09	0.18
Simuliidae indet.	59	0.45**	0.47**	0.37**	0.21
Chironomidae indet.	3268	0.43**	0.43**	0.45**	0.08
<i>Ceratopogonidae</i> indet.	23	-0.07	-0.06	-0.05	-0.15

TABLE 2

The bivariate correlation coefficients between the studied predator categories and some general prey parameters. "Total" refers to all non-predators, while "potential" prey are those categories listed in Table 1. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

	Prey abundance (total)	Prey biomass (total)	Prey biomass (potential)	Prey mean weight (potential)	Prey median weight (potential)
D. cephalotes, large nymphs	0.42**	n.s.	0.50**	n.s.	n.s.
D. cephalotes, small nymphs	0.47**	0.37*	0.49***	n.s.	n.s.
I. grammatica	0.45**	0.31*	0.45**	n.s.	n.s.
R. nubila	n.s.	n.s.	0.45**	0.49***	0.50***

TABLE 3

Group means and standardized discriminant function coefficients for large Dinocras cephalotes (N = 84). The canonical correlation coefficients were for DF 1 and DF 2, 0.70 and 0.54, respectively.

	Density of <u>W. subnigra</u>	Density of <u>H. siltalai</u>	Plecoptera median weight
GROUP MEANS			
Group 1	0.75	0.84	-3.56
Group 2	1.28	0.45	-2.18
Group 3	2.04	2.05	-2.09
STANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS			
DF 1	0.84	0.29	0.04
DF 2	-0.71	0.73	0.78

most in DF 1 were the abundances of Wormaldia subnigra and Hydropsyche siltalai (Tab. 3, Fig. 1A). The second discriminant function (DF 2) separated primarily samples including those microhabitats in which Dinocras was absent from those where it was present (Tab. 3, Fig. 1A). The most important variables in this context were the median size of stonefly prey and the abundance of H. siltalai, which were both positively related to the density of Dinocras. W. subnigra had a negative discriminant function coefficient in DF 2. The group means (Tab. 3) indicate that the

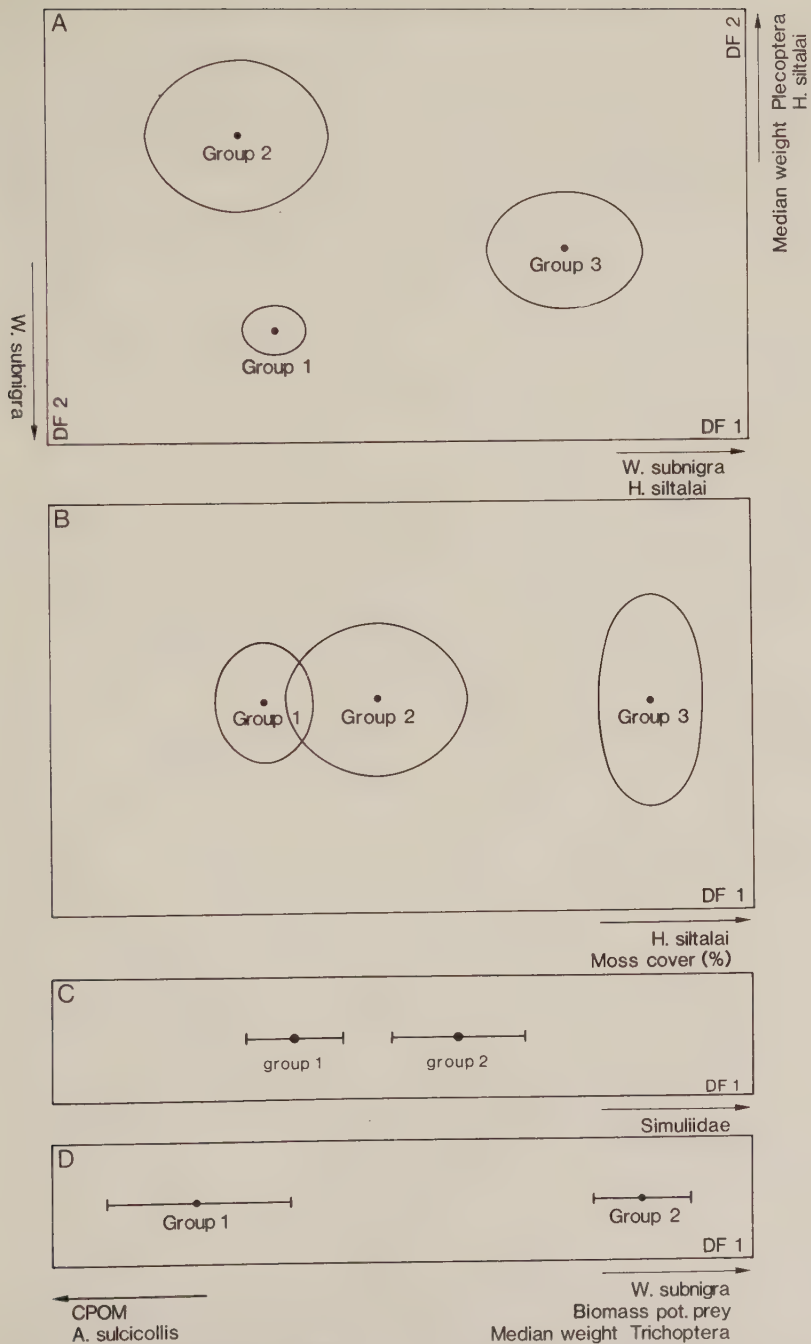


Fig. 1. Plots of group centroids along the discriminant function axes with 95 % confidence limits indicated. A. Large *Dinocras cephalotes* (inter-ocular distance > 1 mm). B. Small *D. cephalotes* (inter-ocular distance < 1 mm). C. *Isoperla grammatica*. D. *Rhyacophila nubila*.

prime importance of this variable was in discriminating Groups 1 and 2 from Group 3.

The main variables incorporated in the discriminant functions for small Dinocras (inter-ocular distance < 1 mm) were the abundance of H. siltalai and the presence of aquatic mosses (Tab. 4, Fig. 1B). The second discriminant function did not significantly add to the discrimination between the groups. Group means indicate that the abundance of H. siltalai was coinciding with high predator density and seemed to be equally important for the separation of the three groups, while the presence of mosses was primarily associated with microhabitats with high densities of small Dinocras nymphs (Tab. 4).

TABLE 4

Group means and standardized discriminant function coefficients for small Dinocras cephalotes (N = 50). The canonical correlation coefficients were for DF 1 and DF 2, 0.65 and 0.001, respectively.

	Density of <u>H. siltalai</u>	Moss cover
GROUP MEANS		
Group 1	0.86	0.31
Group 2	1.38	0.91
Group 3	2.62	2.37
STANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS		
DF 1	0.68	0.59
DF 2	-0.77	0.84

The outcome of the analysis of Rhyacophila nubila showed that this species evidently tends to occur in microhabitats with high biomass of potential prey and large-sized caseless caddislarvae (Tab. 6, Fig. 1D). There were negative correlations with the density of Amphinemura sulcicollis and coarse leaf detritus. The canonical correlation coefficient was comparatively high (0.81) indicating that the variables incorporated in the discriminant model were to a large extent sufficient to explain the observed variation in the occurrence of R. nubila larvae.

In Isoperla grammica the abundance of Simuliidae was the only variable significantly contributing to the discriminant function (Tab. 5, Fig. 1C). The discriminatory power was relatively low.

TABLE 5

Group means and standardized discriminant function coefficients for Isoperla grammatica (N = 50). The canonical correlation coefficient was 0.48.

Density of Simuliidae	
GROUP MEANS	
Group 1	0.48
Group 2	1.31
STANDARDIZED DISCRIMINANT FUNCTION COEFFICIENT	
DF 1	1.00

TABLE 6

Group means and standardized discriminant function coefficients for Rhyacophila nubila (N = 81). The canonical correlation coefficient was 0.81.

	Biomass of potential prey	Presence of coarse detritus	Median weight of Trichoptera	Density of <i>A.sulcicollis</i>	Density of <i>W.subnigra</i>
GROUP MEANS					
Group 1	2.42	1.0	2.18	2.05	0.60
Group 2	3.40	0.5	3.18	2.62	1.58
STANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS					
DF 1	1.30	-0.87	0.72	-0.70	0.61

DISCUSSION

In the bivariate analysis Dinocras cephalotes showed positive correlations to a large number of variables, both biotic and abiotic, out of which only a limited number reappeared in the discriminant analysis. The inherent suppression of covarying factors in this analysis, however, does not necessarily mean that

these variables lack significance in explaining the microdistribution of a species or size category.

The most important variable which contributed to the recognition of Dinocras microhabitats was the abundance of caseless caddislarvae, mainly Hydropsyche siltalai. In a previous study (Sjöström, I) caseless caddislarvae were found to be the dominating food items in terms of weight for large Dinocras nymphs. Also other large perlid stonefly nymphs are reported to feed heavily on larvae of Trichoptera (Sheldon 1969, 1980, Siegfried & Knight 1976, Fuller & Stewart 1977).

The median size of stonefly prey was also incorporated in the discriminant model for large Dinocras. Perlid stonefly nymphs are known to expand the size range of ingested prey as they grow larger (Sheldon 1969, Allan 1982). In D. cephalotes it does not seem to be an expansion of the size range of captures stonefly prey, but rather an increasing size of captured prey so that there was virtually no overlap between small and large nymphs (Sjöström, I).

The presence of mosses was also significant in our attempt in defining the microhabitats of small Dinocras. Mouthon & Vernaux (1979) found that Dinocras megacephala (Klapalek) during most of its nymphal life was associated with moss. Hynes (1941) also reported D. cephalotes to occur in streams with moss covered stones. Moss possibly serves both as shelter and hunting area for small nymphs. Chironomids are, from a quantitative point of view, the most important prey for small Dinocras nymphs (Sjöström, I). One reason for the fact that chironomids did not appear in the discriminant analyses might be the heterogeneity of its availability to the predators and the broad microhabitat choice of this multi-species group.

Isoperla grammatica includes simuliids in its diet (Hynes 1941, Brinck 1949) and the correlation with simuliid distribution was the only significant one in the discriminant analysis. In this context, it is interesting to note that Sheldon & Oswood (1977) found a strong correlation in the longitudinal distribution of Isoperla spp. and simuliids in a North American lake outflow. However, the most frequent food items found in the guts of I. grammatica were reported to be chironomid larvae. Again the computer program did not identify this variable, and the possible reason might be its heterogeneity. Isoperla nymphs ingest also vegetable matter (Hynes 1941, Brinck 1949). Such a

broad food niche might involve a restricted microhabitat specialization.

Members of the rhyacophilid family are known to be predatory, although algae and detritus are incorporated in the diet to a varying extent in different species. R. nubila, which is probably considerably more sluggish than the predacious stoneflies, is reported to feed on various prey items, e.g. larvae of blackflies, chironomids, and caddisflies (Kuusela 1979). Otto (pers. comm.) found frequently non-animal material in their guts. The main prey consisted of Trichoptera, e.g. hydropsychid larvae and baetid mayfly nymphs.

In Klövbäcken the occurrence of R. nubila is strongly associated with patches having high biomass of potential prey, which can be expected for a relatively slow predator. The larvae would also benefit from high median biomass of campodeiform Trichoptera and from high densities of the net-spinning species Wormaldia subnigra. The negative correlation with coarse particulate matter and with the detritivorous stonefly Amphinemura sulcicollis is no casual relationship, but mirrors the distribution of R. nubila which tends to avoid microhabitats where detritus accumulates. R. nubila showed preference for increasing stone size in the bivariate test, which might be equivalent to avoiding detritus aggregations.

There is some controversy whether lotic invertebrate predators gather in aggregations. Hildrew & Townsend (1976) found Plectrocnemia conspersa (Curtis), a sit-and-wait predator (Trichoptera: Polycentropodidae) and the more active megalopteran Sialis fuliginosa Pictet to aggregate in patches rich in prey. Also Fahy (1975), Hawkins & Sedell (1981), and Hawkins et al. (1982) have reported positive correlations between predator and prey densities. On the other hand, Peckarsky and Dodson (1980) failed to find such a response in colonization experiments involving various predators (stoneflies and triclads) at different prey densities. The spatial patterns of the predators in our study clearly imply aggregative responses, both in terms of bivariate correlations (Tab. 2), and the discriminant analyses (Tab. 3-6). The latter analyses showed consistently that various prey characteristics were the most powerful factors in explaining the variation in predator abundance, irrespective of species.

The reason why the distribution of the predators was to a large extent related to caseless caddislarvae or simuliids might

be the relatively sessile life of these animals. It should be more favourable to hunt in these patches than in patches with very mobile prey such as baetid mayflies. Indeed, Molles & Pietruszka (1983) found considerably higher success for two North American perlids in capturing a relatively slow mayfly prey (an Ephemerella species) compared to a faster baetid. Further, within a patch the mobile species tend to fluctuate heavily in density (Wiley & Kohler 1981).

The main conclusion that can be drawn from this study is that biotic factors seem to be of considerable importance for the different patterns in the microdistribution shown by lotic insect predators. Thus, we found that prey size influenced the microdistribution of the predators, but also that other qualitative and quantitative factors, such as the availability of certain prey species and overall measures of potential prey biomass were important. It seems realistic to speculate that not only the properties of the prey community would influence the predator distribution in streams, but also the strategy (e.g. degree of mobility) employed by various predator species.

ACKNOWLEDGEMENTS

We thank Professor P. Brinck for constructive criticism of the manuscript and Mrs S.Douwes for preparing the figure. The study was supported by the Swedish Natural Science Research Council.

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HUNTING BEHAVIOUR OF THE PERLID STONEFLY NYMPH

DINOCRAS CEPHALOTES (PLECOPTERA)

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ABSTRACT

The hunting behaviour of *Dinocras cephalotes* nymphs was studied at two different light regimes viz. darkness and twilight (0.1 cd m^{-2}). Nymphs of the mayfly *Baetis rhodani* were provided as food.

In darkness the predator moved slowly without stops encountering the prey with the antennae and the hair fringes on the tibiae. Little time was spent in the shelter. The propensity to pursue the prey after a missed attack was low and the pursuing distance was short.

At twilight the speed of the predator was higher and the movement was interrupted by long periods of immobility. The number of successful attacks was higher and more attacks were released when the predator was immobile. Time of activity outside the shelter was short. The propensity to pursue the prey after a missed first attack was higher and the pursuing distance was longer compared to darkness.

There are two main advantages of changing strategy from searcher at dark to ambusher at light, viz. to avoid detection by predators hunting by vision and to avoid detection by potential prey species relying on visual cues.

The optical design of the eye revealed that only those parts of the eye directed upwards and backwards were optimized to the light conditions at which the predator was preferably active, indicating the main function to be anti-predatory though an additional gain in prey detection could be seen.

INTRODUCTION

Most aquatic insect predators are considered to detect prey by mechanical cues. Stonefly nymphs of families Perlodidae and Perlidae were reported to search for prey by scanning the substrate with their antennae (Kovalek 1978, Peckarsky 1979).

Visual cues are not thought to be of major significance at prey detection in lotic immature insects (Peckarsky 1982), although most hemimetabolic insect nymphs have prominent optic lobes with a varying number of ommatidia. Some dragonfly nymphs, however, rely to a large extent on visual cues for prey detection and capture (Pritchard 1965, Oakley and Palka 1967).

The compound eye of insects active at twilight must arrive at a compromise between optical resolution and sensitivity to low light intensities. Conflicting demands, e.g. predators versus hunting or search for mates, influence the structure of the eye. Thus, diel activity patterns of insects relying on visual cues should be reflected in the design of their compound eyes. Cf. reviews of insect vision by Horridge (1977, 1980).

Perlid stonefly nymphs are considered to be primarily nocturnal feeders (Hynes 1941, Brinck 1949, Vaught and Stewart 1974). Most conclusions regarding diel feeding patterns in stoneflies were, however, derived from variation in gut content during the day (e.g. Vaught and Stewart 1974, Winterbourn 1974, Johnson 1981 and Allan 1982). In a laboratory experiment, Molles and Pietruszka

(1983) found that two stonefly predators showed the same propensity to attack during day and night, while the activity of Dinocras cephalotes coincided with the dark hours (Müller and Benedetto 1970). Malmqvist and Sjöström (1980) found that Dinocras cephalotes nymphs did not consume any prey during the light hours.

The present study was designed to investigate the hunting behaviour of Dinocras cephalotes in different light regimes and the role played by vision at prey detection.

MATERIAL AND METHODS

The arena used for the behavioural studies, consisted of a plexi-glass aquarium (18 x 15 x 5 cm). Oxygenated and cooled water ($10^{\circ}\text{C} \pm 1^{\circ}$) was pumped through the aquarium. A refuge consisting of a gray ceramic plate (4 x 4 x 1.5 cm) was placed in one corner of the arena. The plate rested on four small stones, leaving a free space of 5 mm.

Luminance (candela m^{-2}) was measured at the bottom of the arena using a photometer. The light source was a halogen lamp (150 W) whose light intensity could be varied. During day time the intensity was regulated so that luminance at the bottom of the arena was 200 cd m^{-2} , while during the experiments it was 0, 0.1 and 0.5 cd m^{-2} , respectively.

The behaviour of the predator and the prey was registered with a video camera, supplied with a vidicon sensitive to light of the infra-red spectrum (Philips LDH 26/02), and recorded on a video recorder (JVC 2200 EG). The infra-red light source emitted light of the wavelength 800 nm with only 1 % of the emitted light in the visible red spectrum.

One Dinocras cephalotes nymph was placed in the arena two days prior to the experiment in order to become acclimatized. During this time no prey was provided. Each experiment consisted of the following sequence of light regimes: total darkness, 0.1 and 0.5 cd m^{-2} . Each light intensity was maintained for one hour. The same nymph was used in five subsequent experiments. Only one experiment per day was performed. A total number of 10 Dinocras nymphs were tested. To facilitate the observations only comparatively large Dinocras nymphs were used. Five nymphs of Baetis rhodani (mean length $7.9 \pm 1.1 \text{ mm}$) were introduced in the beginning of each experiment. The number of prey was kept constant during the different light regimes and at the end of the experiment the remaining specimens were removed.

Times of activity and immobility were registered. The reaction distance of the predator was measured on the monitor screen (the distance on the screen was correlated to actual distance in the arena). The speed of the predator was measured as follows: the moving animal was followed by a planimeter and the time registered on a stop watch. Three measurements were made during each light regime (periods of immobility were not included).

One experiment was performed to investigate if hunger increased the hunting activity at light. Single nymphs were placed in 10 aquaria equipped with shelter as in the arena. The temperature was kept at $10^{\circ}\text{C} \pm 1^{\circ}$. During day time light intensity was 200 cd m^{-2} . For two hours every day the light intensity was lowered to 0.5 cd m^{-2} and the activity of the nymphs was registered. The survival time of the nymphs was recorded.

In order to determine how the compound eye of Dinocras cephalotes works optically the eye was mapped. The head of a newly decapitated nymph was mounted on a goniometer which was placed under a dissecting microscope with light throughcoming from above. The direction of view of each ommatidium was determined using the pseudopupil (see Stavenga 1979) which in incident light appears as a dark spot. The turning angle required to move the centre of the pseudopupil five facets determines the interommatidial angle between every fifth ommatidium (5ϕ). The different ϕ values were plotted on a map in angular coordinates (see Nilsson and Odselius 1982). Because of the difficulty in measuring the aperture of hexagonal lenses, D (μm) was measured as the distance between centres of adjacent facets. Horizontal and vertical planes of the eye were determined by placing the nymph in normal hunting position (Fig. 1). Two rows of facets along the horizontal axis and two rows along the vertical axis of the eye were measured. All measurements were made with the goniometer submerged in water, in order to mimic natural conditions of refraction. The eye parameters, $D\Delta\phi$ (Horridge 1978) of one large and one small nymph were determined. From these values, calculations were made of the optimization of different parts of the eye as regards light intensity according to Snyder (1977). The spatial resolution at different distances from the eye was calculated as follows:

$$B = \sin(R) \times d$$

where B denotes spatial resolution (mm), R angular resolution ($^{\circ}$) and D distance from the ommatidium (cm).

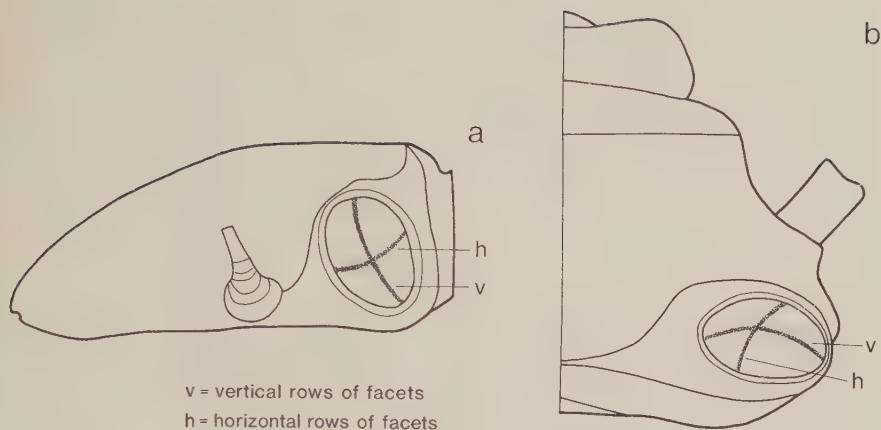


Fig. 1. Lateral (A) and dorsal (B) view of the head of D. cephalotes. The filled lines indicate position of the mapped ommatidia along the horizontal and vertical axis, respectively.

RESULTS

No activity was registered outside the shelter during the light regime of 0.5 cd m^{-2} . Starvation did not increase the propensity to leave the shelter at light. The nymphs remained in their refuge until death. The ability to withstand starvation was, however, high. Half of the nymphs survived for 80 days without food and one nymph was still alive 170 days after the experiment started. Due to the lack of activity only results from light regimes below 0.5 cd m^{-2} are discussed below.

The attack on the prey was usually released by the predator touching it with either the antennae or the hair fringes of the tibiae. Of the total number of attacks observed ($N = 197$), during darkness as well as illumination (0.1 cd m^{-2}), 96 per cent were released by contact with the antennae, while 4 per cent were initiated by contact with the tibian hairs. Tactile stimuli from other parts of the body (e.g. cerci and abdominal sclerites) did not lead to an attack. Once the Dinocras nymph had encountered the prey it quickly turned towards the prey and rapidly rushed forward and grabbed it with the opened maxillae.

In several respects the behaviour of the Dinocras nymphs differed between the two light regimes.

Darkness (0 cd m^{-2})

During darkness the hunting behaviour was rather stereotyped. The nymphs advanced slowly, moving the antennae from side to side and the time spent motionless outside the shelter was short, while total time spent outside the shelter, i.e. time of activity, was long (Tab. 1). During the active period, the time spent under the shelter mostly consisted of passages of the shelter rather

TABLE 1

Comparison of speed, total time spent outside the shelter and time spent immobile outside the shelter for *Dinocras cephalotes* nymphs at two light intensities. The experiments lasted for 60 minutes, respectively.

Students t-test was applied to test for significance.

	Darkness (0 cd m^{-2})			Twilight (0.1 cd m^{-2})			P
	Mean	S.D.	N	Mean	S.D.	N	
Predator speed (cm s^{-1})	0.6 ± 0.17		50	1.0 ± 0.44		30	< 0.001
Total time spent outside the shelter (min)	45.6 ± 10.0		50	7.2 ± 13.2		50	< 0.001
Time spent immobile outside the shelter (%)	5.9 ± 2.1		50	29.0 ± 17.7		30	< 0.001

than periods of rest. The reaction distance did not exceed 1.5 cm. This distance is in accordance with the length of the antennae of the nymphs used in the experiments (mean length 11.7 mm, S.D. 1.3 mm, N = 10). The majority of the attacks were released when the predator was moving, actively searching for prey. Only 12 per cent of the total number of the attacks were released when the nymph was immobile (Fig. 2). In only one case did an attack start from under the shelter (Fig. 3) and in this case the nymph, when passing below the plate, encountered the prey when arriving at the other side. In darkness only 3 per cent of the first attacks which failed were followed by an immediate second attack on the same prey (Fig. 4). The second attacks all failed. In these cases the distance between the first and the second attack did not exceed 2 cm, indicating that the prey was still within the range of the antennae of the predator. Reaction distances which were shorter than 1.5 cm could not be measured accurately, due to the very rapid attacks. During darkness 23 per cent of the attacks were successful (Fig. 5). All encounters released an attack.

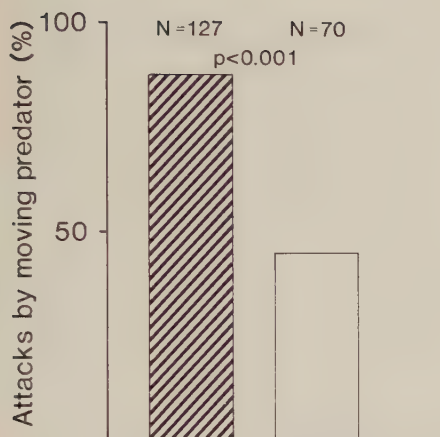


Fig. 2. Attacks released when the predators were actively searching (moving) in darkness (filled bar) and at 0.1 cd m⁻², given as percentage of the total number of attacks. P value was calculated by χ^2 statistics.

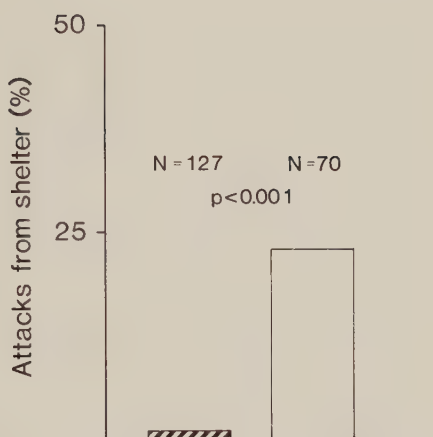


Fig. 3. Attacks released when the predators were under the shelter in darkness (filled bar) and at 0.1 cd m⁻², given as percentage of the total number of attacks. P value was calculated by χ^2 statistics.

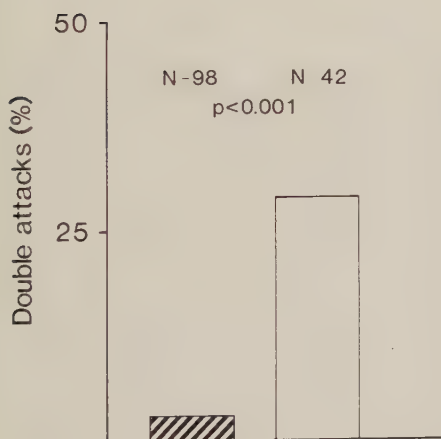


Fig. 4. Second attacks performed after missed first attack in darkness (filled bar) and at 0.1 cd m⁻², given as percentage of the number of missed first attack. P value was calculated by χ^2 statistics.

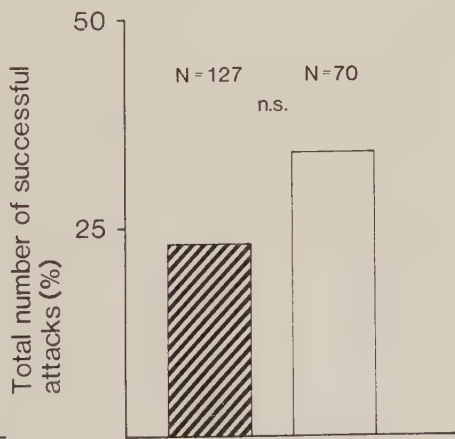


Fig. 5. Total number of successful attacks in darkness (filled bar) and at 0.1 cd m⁻², given as percentage of the total number of attacks. P value was calculated by χ^2 statistics.

Twilight (0.1 cd m^{-2})

At illumination the speed of the predator was significantly higher ($p < 0.001$, t-test) than in the darkness (Tab. 1). The behaviour of the nymphs could be characterized as short rushes interrupted by stops. The total time spent outside the shelter was significantly shorter ($p < 0.001$, t-test), but of this time the predator was significantly more motionless ($p < 0.001$, t-test) than during darkness (Tab. 1).

The mode of attack was the same as in the dark as long as the prey moved along the bottom of the arena, i.e. the attacks were released by contact with the antennae or the hair fringes on the tibiae.

The propensity to attack from stand still was significantly higher ($p < 0.001$, χ^2 -test) than at darkness (Fig. 2). Also the number of attacks performed from the shelter was significantly higher ($p < 0.001$, χ^2 -test) (Fig. 3). If the predator missed the first attack the propensity to pursue the prey and perform a second attack was significantly higher at twilight than during darkness ($p < 0.001$, χ^2 -test) (Fig. 4). The total number of successful attacks was higher at illumination than in darkness (n.s., χ^2 -test) (Fig. 5).

At twilight the Baetis rhodani nymphs fled from the approaching predator before the distance was sufficiently short to enable tactile contact and thereby initiate an attack. Thus the number of successful first attacks was significantly higher ($p < 0.01$, χ^2 -test) when the predator started the attack from stand still than when it was actively searching (Fig. 6). The significantly higher hunting success ($p < 0.05$, χ^2 -test) at the second attack also contributed to the higher total number of successful attacks at twilight (Fig. 7).

The reaction distance for the first attacks performed did not increase compared to the distance at darkness. But the pursuing distance, i.e. the distance between the first and the second attack on the same prey, increased from less than 2 cm to a mean of 3.5 cm (range 2-5 cm). The propensity to pursue the prey was related to the behaviour of the prey at escaping. When the Baetis nymphs were walking or running on the bottom of the arena, the predator did not seem to detect them, but when they were swimming the propensity to perform a second attack towards the escaping prey increased.

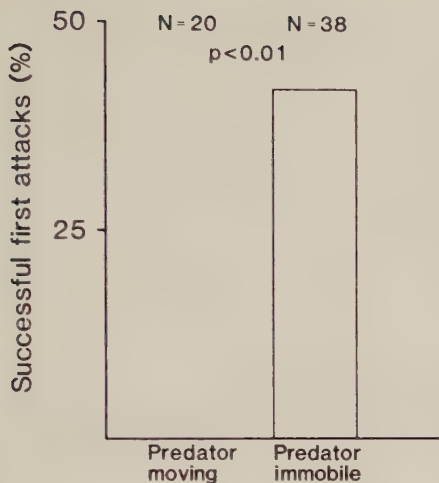


Fig. 6. Number of successful first attacks at 0.1 cd m^{-2} , given as percentages of number of first attacks performed when the predators were moving or immobile. P value was calculated by χ^2 statistics.

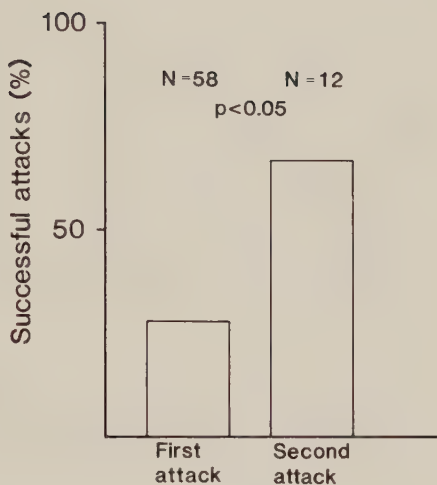


Fig. 7. Number of successful attacks at 0.1 cd m^{-2} , given as percentages of numbers of first and second attacks, respectively. P value was calculated by χ^2 statistics.

Optical design of the eye

The eye parameters $D \emptyset$ of the ommatidia along the horizontal axis are shown in Fig. 8A and the corresponding values for the vertical axis in Fig. 8B. The angular resolution displays the highest values in the anterior part of the eye where the ommatidia are directed forward and downward (Fig. 9A). In addition, the eye parameter values show this part of the eye to be optimized to comparatively high light intensities ($1 - 2.5 \text{ cd m}^{-2}$). But when moving along the horizontal axis to the posterior parts of the eye where the ommatidia are directed upward and backward, the resolution decreases, while the ommatidia become gradually designed to lower light intensities (0.05 cd m^{-2}). The eye parameters of the ommatidia along the vertical axis vary less and resolution and light optimization remain fairly constant in ventral and dorsal parts of the eye. The pattern is similar in both small and large nymphs, though lack of space diminishes the number of ommatidia in small nymphs (Figs 8-9).

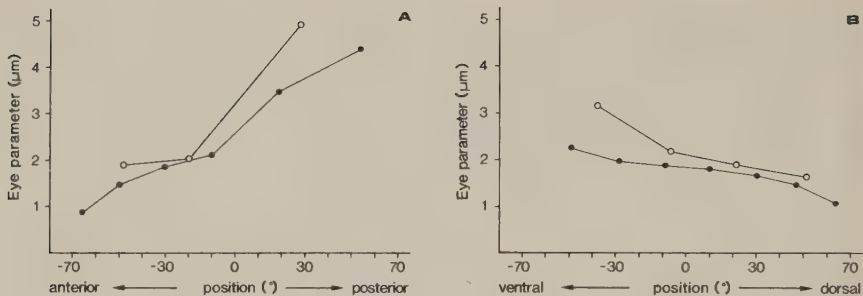


Fig. 8 Eye parameter values of ommatidia at different positions along (A) the horizontal axis, zero denotes position perpendicular to the longitudinal axis, and (B) the vertical axis, zero denotes position in the horizontal plane. Filled circles denote large animal and unfilled circles denote small animal.

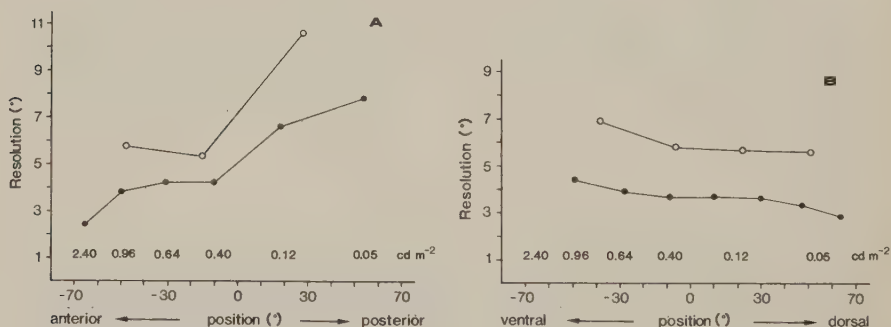


Fig. 9. Angular resolution and light optimization of ommatidia at different positions along (A) the horizontal axis, zero denotes position perpendicular to the longitudinal axis of the animal, and (B) the vertical axis, zero denotes position in the horizontal plane. Filled circles denote large animal and unfilled circles denote small animal.

Only the posterior parts of the eye were optimized to the light conditions which prevailed during the experiments (Fig. 10). In addition, the ability to detect small objects was at its lowest in these parts of the eye. The ability to detect small objects depends, however, not only on the aperture of the ommatidia but also on the contrast between the object and the background.

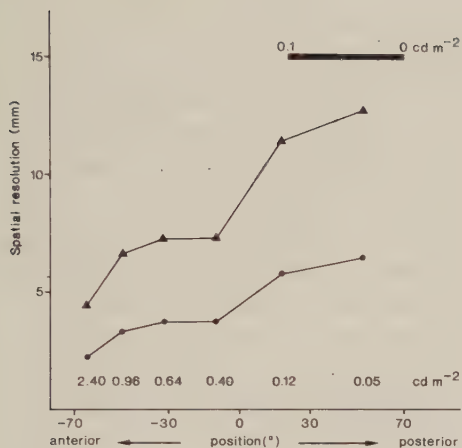


Fig. 10. Spatial resolution at two distances from the eye and light optimization of ommatidia along the horizontal axis. Zero denotes position perpendicular to the longitudinal axis of the animal. Filled circles denote distance of 5 cm and triangles denote distance of 10 cm from the eye. The light conditions prevailing during the experiments are indicated with a black bar.

DISCUSSION

In spite of slightly increased hunting success at twilight the propensity to hide in the refuge was strong. Severe starvation did not increase the propensity to hunt at light. Thus, it seems likely that Dinocras cephalotes nymphs are active exclusively during the dark hours. The two predatory stonefly species studied by Molles and Pietruszka (1983) showed the same propensity to attack at day light as in darkness which made the authors to perform their studies of hunting behaviour at day light. Denying the nymphs a refuge at light may, however, change the natural hunting behaviour. When Dinocras cephalotes nymphs were observed at full light (200 cd m^{-2}) and no shelter was available their behaviour was completely different compared to that at dark or twilight, i.e. running quickly along the sides of the arena without stops. When encountering a prey the propensity to attack, however, remains.

The strong propensity to hide at light showed by Dinocras nymphs indicates that hunting at darkness is safer than at light. When hunting is carried out at the low light intensities of 0.1 cd m^{-2} the eye is sensitive only in the parts directed upwards and backwards, indicating that their main functional role is to detect predators. It is true that in these parts of the eye the resolution is low (Fig. 9), but it seems that the only predators capable of overpowering at least large Dinocras nymphs

should be comparatively large, under present conditions salmonid fish which prevail in Dinocras habitats.

Although optimized to low light intensities, these upward and backward directed parts of the eye can serve as a complement in detecting prey items. When the prey tries to escape by swimming up in the water column, it may eventually enter the visual field of these parts of the eye thus making it possible for the predator to detect and pursue the prey. On the other hand, when the prey escapes along the bottom it remains within the visual field of the ommatidia which are not optimized to such low light intensities. That is probably the reason why Dinocras nymphs respond only to tactile cues when the prey is moving on the bottom.

Peckarsky (1982) classified aquatic insect predators into two main categories according to their mode of prey encounter: ambushers ("sit and wait") stay motionless before the attack until a suitable prey is near, while searchers actively move around on the substrate in order to find the prey. Thompson (1978) and Corbet (1980) described how hunger could cause damselfly nymphs to give up their ambush strategy and actively search for prey.

In Dinocras nymphs there are two advantages of changing strategy from searcher to ambusher when light intensity increases. Swift and short rushes interrupted by long periods of immobility will minimize the risk of being detected and attacked by a fish predator. Salmonids are known to hunt mainly by means of visual cues and a prerequisite for attack is movement of the prey (Chapman 1966, Otto and Sjöström in press). The other advantage of periods of immobility is that a prey relying on visual cues (cf. Peckarsky 1980) does not detect the Dinocras nymph until the attack starts.

ACKNOWLEDGEMENTS

I wish to thank Dr. D.-E. Nilsson who performed the optical measurements. I am also grateful to Prof. P. Brinck, Dr. L.M. Nilsson and Dr. C. Otto for valuable criticism of the manuscript. S. Douwes kindly drew the figures and Y. Zachrisson typed the manuscript. Financial support was provided by grants from the Swedish Research Council (to B. Malmqvist).

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TERRITORIALITY IN NYMPHS OF DINOCRAS CEPHALOTES (PLECOPTERA)

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ABSTRACT

Interference between Dinocras cephalotes nymphs of equal size was studied in both retreats and hunting area. Three nymphs were successively introduced into the aquarium and their choice of shelters and aggressive behaviour was registered.

The nymphs first introduced preferred to spend the light hours in the large retreat and did successfully keep away intruders as did they win most contests in the hunting area. The second introduced nymphs were confined to the small retreat which they successfully defended against both first and third introduced nymphs. The third introduced nymphs did not get access to any of the two retreats and did also loose contests with first and second nymphs in the hunting area. When the large retreat was removed the first introduced nymph subsequently invaded the remaining retreat and forced the second nymph to spend the light hours outside the retreat in the hunting area. Aggressive behaviour decreased from the first to third introduced nymphs.

The territorial behaviour is suggested to act as an important spacing factor in nymphs of D. cephalotes.

INTRODUCTION

Studies of insect territoriality have to a large extent been focused on males defending sites related to reproduction. The defence of other resources, e.g. food and shelter, has been demonstrated mainly in social insect species. A review of territoriality in insects was given by Baker (1983).

Similarly intra specific interference among lotic insects was investigated only rarely. Hildrew and Townsend (1980) showed that larvae of the net-spinning caddisfly Plectrocnemia conspersa (Curtis) contest the ownership of their nets and that the outcome was determined mainly by the body size of the larvae. Peckarsky and Dodson (1980) suggested that the lack of observable aggregation among predators in a colonization experiment could be explained by mutual interference. Walton et al. (1977) suggested that in a laboratory experiment the densities of the nymphs of the perlid stonefly Acroneuria abnormis (Neuman) were influenced both by the number of crevices suitable as shelter and individual interferences.

Nymphs of the perlid stonefly Dinocras cephalotes (Curtis) are predators with comparatively large mandibles which may serve as effective weapons to keep intruders from a defendable resource. This study investigates whether the nymphs show aggressive behaviour towards conspecifics and whether they contest ownership of resources such as shelter and hunting area.

MATERIAL AND METHODS

The studies of the nymphs were performed in a plexiglass aquarium (18 x 15.5 cm) through which aerated and cooled water ($10^{\circ}\text{C} \pm 1^{\circ}$) was pumped. Two gray ceramic plates served as shelters, placed in each corner of the aquarium. They were 4 x 4 x 1 cm and 3 x 2.5 x 1 cm and rested on four small stones, leaving a space of 5 mm.

The behaviour of the nymphs was registered with a videocamera supplied with a vidicon sensitive to light of the infra-red spectrum (Philips LDH 26/02) and recorded on a video tape recorder (JVC 2200 EG). The infra-red light source emitted light of the wavelength 800 nm with only 1 % of the emitted light in the visible red spectrum.

The behaviour of the nymphs was registered in darkness during one hour. Then, in order to force the nymphs to shelter, the light intensity was raised to 0.1 cd m^{-2} and the behaviour of the nymphs was registered for one hour. Only one sequence of recordings was carried out per day. Between the recordings dim daylight conditions were maintained by means of a halogen lamp (150 W). Each experiment lasted 12 days and no food was provided.

The experiments were performed as follows. One nymph was placed in the aquarium and its choice of shelter was registered during four subsequent days. Then a second nymph was introduced and the interactions between the nymphs as well as their respective choices of shelter were registered during the next four days. Six pairs of nymphs were tested in this way. After these recordings, the largest shelter was removed from three of the aquaria, and interactions were registered during four days. In the other three aquaria both shelters remained but a third nymph was introduced and the interactions and the choices of shelter were registered during the last four days of the experiment. In each experiment the nymphs were of equal size: the mean interocular distance was 3.8 mm ($N = 15$).

RESULTS

When the first nymph was alone in the arena, it preferred the larger shelter in the light hours (Tab. 1). When the second nymph was introduced, the first one resided in the large shelter, while the second nymph was confined to the small shelter (Tab. 1). Neither the first nymph nor the second stayed outside the shelters in daytime or together in the same shelter. When a third nymph was

TABLE 1

Number of days spent in shelters by the *Dinocras* nymphs. P values were calculated by χ^2 , expecting equal choice between the large and small shelter.

	Large shelter (days)	Small shelter (days)	N	χ^2	P
First nymph alone	22	2	24	16.67	< 0.001
First and second nymph together	19	5	24	8.17	< 0.01
First, second and third nymphs together	11	1	12	8.33	< 0.01

introduced it never got access to shelter (N = 12 days), and the nymph spent the days immobile either in the hunting area or on the top of one of the shelters.

When two nymphs were present in an arena and the large shelter was removed the nymph first introduced invaded the remaining small shelter whose resident nymph was extruded in all days but one (N = 12). The nymph introduced later had to spend the light hours outside the shelter.

The interactions between the two nymphs are illustrated in Fig. 1. In the hunting area and in the large shelter the nymph first introduced won almost all the contests while the nymph introduced later won most of the contests in the small shelter. The majority of the interferences in the shelters took place either when the light was switched off to darkness and recording started or at twilight. In the intervenient dark period, when the nymphs were hunting, the shelters did not serve as retreats but rather as part of the hunting area. Consequently, most of the contests won by the first nymph in the small shelter took place during this period (Fig. 1).

The third nymph introduced in the arena lost all contests (N = 40) in both shelters. In the hunting area it lost all contests with the first nymph, while in contests with the second nymph 64 per cent were lost (N = 22). When the large shelter was removed the first nymph tried to get access to the remaining shelter. At first the second nymph was successful in defending the shelter but after several lost attempts (4-15) the first nymph established itself permanently under the shelter and the second nymph did not win any subsequent contests.

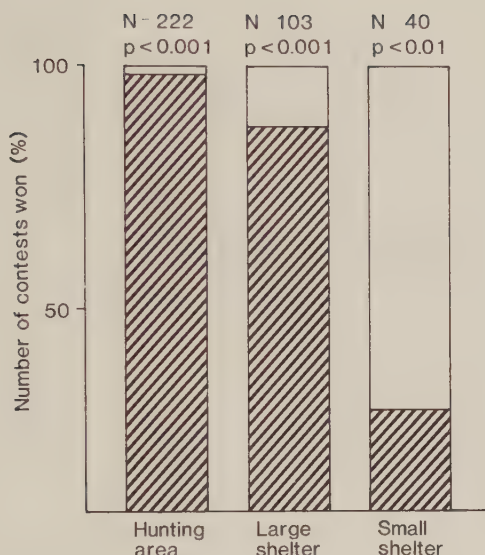


Fig. 1. Number of contests won by the nymph first introduced (filled bars) and the second nymph (open bars) in the hunting area, the large and the small shelters, respectively. P values were calculated by χ^2 , expecting equal numbers of contests won by the first and second nymphs.

The behaviour of the nymphs during contests were classified according to increasing escalation of aggression (Tab. 2). It was not possible to see the behaviour when the nymphs met under the shelters. In the hunting area the nymph first introduced showed the most aggressive behaviour in contests with both the second and third nymphs and it lost few contests as a consequence of the aggressive behaviour of the other nymphs (Tabs 2A, 2B). Again, it lost few contests as a consequence of encounters when no aggressive behaviour was shown by the other nymphs. The majority of the contests between the second and third nymphs were settled without an aggressive behaviour of any of the two nymphs. However, those attacks that did exist were directed from the second towards the third nymph (Tab. 2C).

DISCUSSION

There might be several reasons why the nymphs first introduced choose the large shelter. Oxygen conditions might be better due to increased water circulation. The larger space might facilitate

TABLE 2

Interactions between Dinocras nymphs in the hunting area.

TABLE 2A

Interactions between first and second nymphs, given as percentages of total number of interactions (N = 233).

Type of interaction	No loser	Loser	
		First nymph	Second nymph
Both withdraw without attacking	5		
Withdrawal without attacks		1.5	50
Withdrawal after attacks		0.5	43

TABLE 2B

Interactions between first and third nymphs, given as percentages of total number of interactions (N = 48).

Type of interaction	No loser	Loser	
		First nymph	Third nymph
Withdrawal without attacks			4
Withdrawal after attacks			96

TABLE 2C

Interactions between second and third nymphs, given as percentages of total number of interactions (N = 22).

Type of interactions	No loser	Loser	
		Second nymph	Third nymph
Both withdraw without attacking	18		
Withdrawal without attacks		36	18
Withdrawal after attacks			28

catching prey (cf. Sjöström paper IV). There were comparatively few contests under the small shelter compared to the large one and the free hunting area. A nymph residing in the large shelter apparently rarely approached a resident in the small shelter. But when the large shelter was removed its former resident repeatedly tried to get access to the remaining shelter whose inhabitant subsequently lost residence.

As far as could be seen, the encounters did not result in injuries, though fight occasionally lasted for several seconds and the nymphs frequently attacked the cerci and the antennae of the combatants.

It has been suggested that in territorial animals disputing access to a resource, selection should favour conflict solving processes that minimize the costs of both contestants (review, see Baker 1983). Maynard Smith and Parker (1976) suggested that contestants assess the asymmetries between them which influence the costs and benefits of the contests. Two types of asymmetry might be important, viz. asymmetry in the fighting ability and asymmetry in the value of the resource. This model of conflict solving seems applicable to the territorial behaviour of the nymphs of D. cephalotes. The nymphs that were winners in the large shelter and the hunting area, i.e. the resources chosen by the nymphs first introduced, had the best fighting ability. The asymmetry in fighting ability seemed to be determined by the order in which the nymphs came in to possession of the resources. The second nymphs in the arena were confined to a suboptimal resource, i.e. the small shelter, while the third nymphs had no access to any of the resources. The propensity to avoid conflicts, consequently, increased through the series of nymphs introduced into the arena.

Minor differences in the size of the nymphs did not seem to influence the asymmetries in fighting ability. But large size differences would probably give the largest nymph the best fighting ability regardless of which nymph first entered the arena. One experiment was performed with nymphs of different sizes. The intruder was considerably larger (interocular distance 4.0 mm) than the resident (interocular distance 3.5 mm). The first and second day the residing nymph resisted all attempts from the intruder to get access to the large shelter. The first introduced nymph also won most of the contests in the hunting area. But after two days the intruder invaded the large shelter and held it

for the rest of the experiment. In addition, the intruder now won most of the contests in the hunting area.

To conclude, the nymphs showed a strong propensity to defend their retreats as well as the hunting area surrounding it. This territorial behaviour could certainly act as an important factor in determining the spatial distribution of nymphs of D. cephalotes.

ACKNOWLEDGEMENTS

I thank Professor Per Brinck who gave valuable criticism of the manuscript and provided working facilities. I am also grateful to Mrs Steffi Douwes who drew the figure and to Mrs Ylva Zachrison who typed the manuscript. Financial support was provided by grants from the Swedish Natural Science Research Council (to B. Malmqvist).

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Cerci as antipredatory attributes in stonefly nymphs

Christian Otto and Per Sjöström

Otto, C. and Sjöström, P. 1983. Cerci as antipredatory attributes in stonefly nymphs. – *Oikos* 41: 000–000.

Brown trout *Salmo trutta* were offered *Taeniopteryx nebulosa* and *Dinocras cephalotes* nymphs. Many nymphs were not devoured when attacked but ejected alive. A high proportion of the nymphs feigned dead after ejection. The attacks were preferably directed from the front when intact nymphs were offered. Handling time was longer when the nymphs were attacked from the least preferred direction, and when attacked from this direction a high proportion of the nymphs were ejected. We suggest cerci in stonefly nymphs to be viewed as physical attributes of defensive function, and this function may be an exaptation.

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Accepted 29 September 1982

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Introduction

Adaptation may be defined as anything that confers a survival advantage on an organism (Bock 1979). Gould and Vrba (1982) distinguish adaptations from "exaptations". Adaptations are features which have been directly constructed through natural selection. Exaptations are features which have been coopted into their current use from different previous uses or from structures without any previous function. The presence of cerci is a feature common to many primitive insects. Plecoptera is an ancient insect order, and it is traced back to the Permian period. Many of the morphological attributes found in the stonefly nymphs have been relatively unmodified through time (Illies 1965). Since modern predaceous teleosts did not appear until the Cretaceous period, physical features present in ancient stonefly nymphs can not be antipredatory adaptations (sensu Gould and Vrba) mediated through fish predation. Features may however be exaptations (sensu Gould and Vrba) contributing to an organism's fitness by reducing fish predation.

A physical feature in common to mayfly and stonefly nymphs in lentic as well as lotic waters is the presence of cerci. Usually mayflies have three caudal filaments while stoneflies have two. Many mayfly nymphs swim (often in short bursts) by moving their filaments in a dorsoventral fashion, and the efficiency is enhanced by rows of long hairs bordering the filaments (Hynes 1970). Hynes (1970) proposed that the "long tails" in adult baetid mayflies are important in stabilizing the rather clumsy flight in these insects. Corkum and Clifford (1981) recently investigated potential functions of caudal filaments in two mayfly species. They concluded that the caudal filaments did not effectively deter stonefly predators or aid in moulting. Stonefly nymphs are not as good swimmers as most mayflies and move their cerci laterally when they slowly take off; nor do cerci of stoneflies possess longitudinal rows of hairs as in the mayflies. Some adult stoneflies have their cerci transformed into sexual structures. In those that have cerci any stabilizing effect from these relatively short and stout appendages during flight is unlikely. Hynes (1970) suggested cerci in stonefly nymphs to act as vanes turning the heads of the nymphs into the current. A similar function has been attributed to the presence of long sticks on some caddis cases (Nielsen 1942). Be-

cause turbulence will limit the value of vanes (cf. Otto and Svensson 1980), and as many species dwell in macrophyte vegetation where the current is too weak to turn the nymphs, or in lentic habitats (cf. Brinck 1952), we reject this hypothesis. In stonefly nymphs cerci probably are adaptations of sensory functions, and they may also act as balancing structures when walking or swimming.

In caddis larvae, case enlargement has been shown to reduce vulnerability to fish predators (Otto and Svensson 1980). In stoneflies we suggest cerci to be viewed as antipredatory exaptations giving the nymph a large appearance. Thus, because of the cerci, the nymph may be avoided by some predators. Alternatively, the handling procedure following upon an attack is too costly to make the prey item profitable, and therefore it will be rejected - sometimes alive. Further, cerci may assist in making a threat posture effective. To test these hypotheses the present study was performed.

Material and methods

Brown trout *Salmo trutta* L. are known to prey on stonefly nymphs (e.g. Otto 1976), and wild caught 0+ brown trout (7-9 cm) were used as predators. Eight trout were placed separately in plastic aquaria (30 x 20, height 15 cm) through which water ($10 \pm 1^\circ\text{C}$) was circulated. Besides the stonefly nymphs used during the experiments, the only food items given to the trout were medium sized *Gammarus pulex* L. Intact nymphs of *Taeniopteryx nebulosa* L. (Taeniopterygidae) and *Dinocras cephalotes* Curt. (Perlidae) of similar length and nymphs where cerci or antennae, respectively, had been cut off were given one by one to the trout, and the behaviour of the nymphs and the trout were noted for each attack. Attack was defined as the trout holding at least one half of the nymph in its mouth as a result of its capturing effort. If more than three seconds elapsed between the attacks they were regarded as separate attacks. Length and weight of the nymphs used in the experiments are given in Tab. 1.

Results

Most intact specimens of *T. nebulosa* were devoured immediately when attacked (Fig. 1). On the other hand, in *D. cephalotes* most attacks led to ejection of the prey

Tab. 1. Length and weight (60°C dry wt) of *T. nebulosa* and *D. cephalotes* nymphs used in the experiments. Ten nymphs per species were measured and weighed.

	Antenna		Length (mm)				Total		Weight (mg)	
	$\bar{X}$	S.D.	$\bar{X}$ Body	S.D.	$\bar{X}$ Cercus	S.D.	$\bar{X}$	S.D.	$\bar{X}$ Total	S.D.
<i>T. nebulosa</i>	6.8	0.4	8.4	0.4	5.4	0.5	20.7	0.8	2.6	0.7
<i>D. cephalotes</i>	6.0	0.6	9.4	0.8	6.0	0.6	21.3	1.4	7.3	1.9

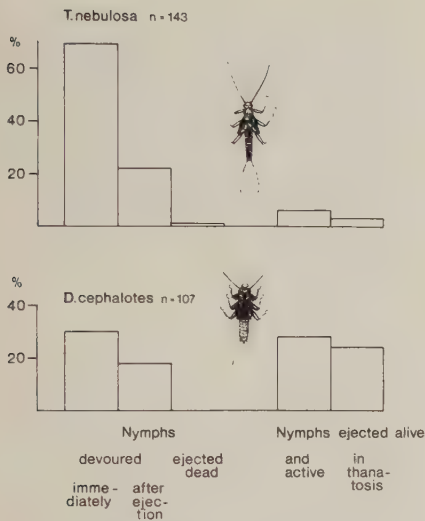


Fig. 1. Effects on intact *T. nebulosa* and *D. cephalotes* nymphs, respectively, of attacks (n) from brown trout.

item (Fig. 1). Some of the ejected nymphs were taken again within three seconds and then devoured, while others were ejected alive and not reattacked. Only a small minority of the nymphs were ejected dead or dying and not reattacked (*T. nebulosa*). Nymphs ejected alive behaved in two fundamentally different ways: some nymphs were active upon ejection while others feigned dead (thanatosis). When in thanatosis *T. nebulosa* nymphs were quite motionless directly upon ejection, and they sank through the water column usually with their legs, antennae and cerci spread out. When these nymphs reached the bottom they rested motionless in whichever position they landed. In *T. nebulosa* nymphs the average time spent in thanatosis was 42 s ($n = 3$). Contrary to *T. nebulosa*, nymphs of *D. cephalotes* when ejected showed a propensity for "swimming" downwards prior to thanatosis. Also in *D. cephalotes* the position on the bottom when in thanatosis was variable. The average time spent in thanatosis was 217 s (S.D. = 187, $n = 24$). Frequency of thanatosis behaviour was high in *D. cephalotes* compared to *T. nebulosa* (Fig. 1).

T. nebulosa

On the bottom intact *T. nebulosa* nymphs as well as those without antennae were preferably attacked from the front. However, the differences in direction were not significant. In nymphs without cerci no preference regarding direction of attacks was observed (Fig. 2a).

Handling time, as calculated from the total number of observations, was significantly longer when intact *T. nebulosa* nymphs were attacked from behind compared to attacks from the front. In nymphs without cerci or antennae no significant difference in handling time was observed with respect to direction of attack (Fig. 2b). When attacked from the front handling time was longest in the intact nymphs, while it was shorter in nymphs without cerci (t-test, n.s.) or antennae ($P < 0.05$). Also consumption of intact nymphs took longer when attacked from behind while the handling time was significantly shorter in nymphs without cerci ($P < 0.001$) or antennae ($P < 0.05$).

In intact *T. nebulosa* nymphs as well as those without antennae ejection was significantly more frequent when the nymphs were attacked from behind. In nymphs without cerci ejection was more frequent, although not significantly so, when they were attacked from the front compared to behind (Fig. 2c).

D. cephalotes

As in *T. nebulosa*, intact *D. cephalotes* nymphs as well as nymphs without antennae were preferably attacked from the front. Unlike *T. nebulosa*, the opposite direction was preferred in nymphs without cerci (Fig. 3a). These differences all were significant if the expectation

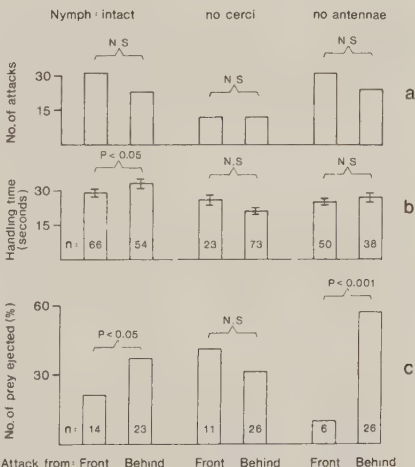


Fig. 2a. No. of attacks from in front and behind, respectively, when *T. nebulosa* nymphs of different appearance were attacked on the bottom. b. Handling time, n refers to total no. of observations and vertical bars denote S.E. c. Percentage amount of prey items ejected (n) out of total captures. In a and c P values were calculated by χ^2 , in a expecting equal frequency from front and behind, respectively, and in b a t-test was used.

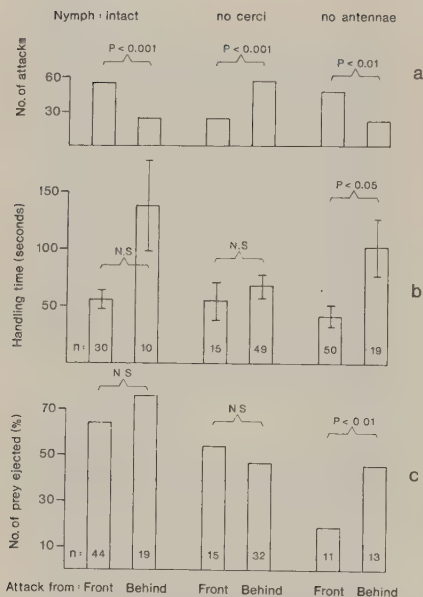


Fig. 3a. No. of attacks from in front and behind, respectively, when *D. cephalotes* nymphs of different appearance were attacked on the bottom. b. Handling time. n refers to total no. of observations and vertical bars denote S.E. c. Percentage amount of prey items ejected (n) out of total captures. In a and c P values were calculated by χ^2 , in a expecting equal frequency from front and behind, respectively, and in b a t-test was used.

was an equal number of attacks from the front and behind.

In *D. cephalotes* handling times were markedly longer than for *T. nebulosa*, and also showed great variation within each nymphal category. We terminated our observations at a maximum handling time of seven minutes, and, as a result, a total of ten observations, evenly distributed among the intact and "cut" nymphal categories, were dismissed with respect to handling time. The longest handling time observed was 29 min. Intact nymphs as well as those without antennae showed long handling times when attacked from behind (Fig. 3b). When attacked from the front or behind, respectively, no significant differences (t-test) in handling time were observed between the intact and "cut" nymphal categories.

Compared with *T. nebulosa*, nymphs of *D. cephalotes* were more frequently ejected, the only exception being nymphs without antennae attacked from behind (Fig. 2c vs. 3c). The percentage of *D. cephalotes* nymphs ejected

was high when intact nymphs and those without antennae were attacked from behind compared to attacks from the front (Fig. 3c). In nymphs without cerci a somewhat higher number were ejected when attacked from the front compared to from behind (Fig. 3c). Most intact nymphs ejected after 15 min and more were alive.

To sum up, brown trout preferably attacked the stonefly nymphs from the front when intact or without antennae, but the other direction was preferred when the cerci were cut off (*D. cephalotes*). Handling time was longer when the nymphs were attacked from the least preferred direction, and then a high proportion of the nymphs were ejected.

Discussion

T. nebulosa is detritivorous while *D. cephalotes* is predaceous. *T. nebulosa* is often found in withering vegetation along the banks of streams where the current velocity is weak. *D. cephalotes*, on the other hand, prefers a stony substrate where the current velocity is much higher. Both microhabitats are often visited by trout, and one would expect selection pressures exerted by this common predator to lead to behavioural as well as morphological antipredatory attributes in both species. Since *D. cephalotes* is a searcher (P. Sjöström unpubl.), and has a life cycle lasting for three years, while *T. nebulosa* is univoltine (Brinck 1952), we suggest the selection pressure for defence to be most intense in *D. cephalotes* being exposed as a potential prey for a long period of time. Nymphs of *D. cephalotes* are stout and heavily chitinated compared with *T. nebulosa*, and at similar length *D. cephalotes* nymphs are much heavier. These attributes are probably responsible for the differences in ejection frequency between the two species. In *D. cephalotes*, these traits may be important to increase the resistance against substrate movements during spates. However, they can also be viewed as antipredatory exaptations. *T. nebulosa* nymphs have projections pointing backwards on the abdominal terga, and these projections may well contribute to reduce the vulnerability of the nymphs to predators.

The differences in thanatosis behaviour probably reflect adaptations to the different current regimes in the stoneflies' microhabitats. Thus, the weak current surrounding *T. nebulosa* will not carry the nymph away when ejected, but it sinks immediately to the bottom. Since movement of the prey item (inclusive of drifting) is known to be a prerequisite for salmonids to attack (Chapman 1966), thanatosis following directly upon ejection should greatly increase the survival rate provided the prey is not moved by the current. In *D. cephalotes* on the other hand, living in exposed microhabitats, the current will immediately move the nymph (drift) after ejection, and thanatosis is of limited value until the bottom is reached. When ejected the nymphs of *T. nebulosa* usually sank motionless with

their antennae, legs and cerci spread out. However, some nymphs curved like an U with their backs towards the bottom while sinking, and these nymphs reduced the time spent passively moving through the water column. *D. cephalotes*, on the other hand, performed "swimming" to reach the bottom as soon as possible after ejection. These observations conform to the behaviour following upon introduction into the aquaria.

By increasing its apparent size (deimatic behaviour) in a "scorpion" display mayfly nymphs are known to lower their vulnerability when attacked by invertebrate predators (Peckarsky 1980). When brown trout attacked the nymphs in this study this posture was sometimes observed when attacked from the front but almost exclusively when the nymphs were half way into the trout's mouth. If this posture is beneficial upon an attack, for example, because it may possibly result in ejection, then, as a "first step" indicating hesitation by the predator, nymphs without cerci (small apparent size) should have a shorter handling time compared with intact nymphs. This was not the case.

A stonefly nymph is more or less shaped like an X, and apparently cerci as well as antennae lower the nymph's vulnerability to fish predators. However, the primary functions of antennae are probably of chemosensory nature. Functions of cerci may also be of sensory origin. In butterflies the presence of "wing tails" diverting a predator's attack towards the less vulnerable end of the insect has led to the "false head" hypothesis (see Robbins 1981). In stonefly nymphs, however the "tails" did not direct the attacks of the trout to the rear end, but rather increased the apparent size of the nymph when viewed from behind and lowered the number of attacks from behind. Therefore the false head hypothesis is not applicable. Besides giving the nymph a large apparent size, cerci in *D. cephalotes* may also contribute to making the nymphs hard to capture when they attach themselves to the (stony) substrate. Thus, the hind part of the nymph including the cerci gently slopes towards the substrate, making the nymph difficult to grasp for the predator.

The presence of "spines" is a widely adopted anti-predatory strategy (Edmonds 1974). In freshwater animals several studies emphasize the importance of this attribute. Ithus Hoogland et al. (1957) showed that pike (*Esox lucius* L.) preferred minnows (*Phoxinus phoxinus* L.) to tenspined (*Pygosteus pungitius* L.) and three-spined sticklebacks (*Gasterosteus aculeatus* L.). Also in *Daphnia* sp. "crest" formation has been shown to lower susceptibility to predators (Grant and Bayly 1981,

Krueger and Dodson 1981). In the stonefly nymphs here investigated attacks from behind more often ended up in ejections of intact specimens compared with ones deprived of their cerci (χ^2 , $P < 0.001$, *D. cephalotes*). Since ejection following upon an attack is bound to enhance the survival rate, we suggest cerci in stonefly nymphs to be viewed as exaptations acting as physical structures of defensive function.

Acknowledgements – We thank B. Peckarsky, Cornell Univ., for comments on the manuscript. A. Ulstrand made the drawings. Support was received from the Swedish Natural Science Research Council.

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